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GEOGRAPHICAL DISTRIBUTION

SYMPOSIUM ON GEOGRAPHICAL DISTRIBUTION PRESENTED BEFORE A JOINT SESSION OF THE AMERICAN SOCIETY OF ZOOLOGISTS, THE AMERICAN SOCIETY OF NATURALISTS AND THE ECOLOGICAL SOCIETY OF AMERICA [1]

GEOGRAPHIC DISTRIBUTION OF CERTAIN NEW ENGLAND MAMMALS

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THE earlier students of geographic distribution, on account of their more limited knowledge of the vertebrate population of the world, were concerned largely with dividing the land masses into realms and provinces which were characterized more or less by the general facies of their faunas. They endeavored to limit these areas by sharply defined boundaries or lines, each to stand, as it were, a sort of zoological Verdun, against which should be written in large letters: "They shall not pass." In later days, with improved methods for intensive collecting, our knowledge particularly of the small mammals has increased a thousandfold, so that the data now at hand are vastly more ample than they were even fifty years ago. We have learned that many of the cherished "lines" and "provinces" are not as clearly marked off as was at first supposed.

[1] Cambridge meeting, December 29, 1922. The remaining papers will be printed in the issue of THE AMERICAN NATURALIST for May–June.

Two of the pioneers in the modern study of smaller mammals in North America, Dr. C. Hart Merriam and the late Dr. J. A. Allen, have both made extensive contributions to the more exact knowledge of the general distribution of the species on this continent, and have endeavored to define certain climatic zones and their subdivisions, and to refer to each a number of species of birds and mammals that seemed characteristic. Their work is well known and need not be further reviewed beyond saying that Merriam's divisions of North America are tacitly adopted by a certain present-day school of field naturalists as fitting the facts in a general way. These so-called life-zones are really transcontinental and altitudinal temperature belts and are subdivided according to their aridity or humidity. But although temperature is an important element in geographic distribution, it is after all but one of many determining factors. In a country of high mountains, the altitudinal zones, corresponding to the latitudinal belts of the continent, are often sharply defined, and have been ably studied in California by Dr. Joseph Grinnell and his associates. In the eastern United States, however, and more particularly in the New England area, where the greatest altitude is but little over six thousand feet, the transition from warm southern climate to cooler temperatures of the north is very gradual, so that the contrasts in faunas are nowhere very sharp.

In any thorough study of the distribution of the mammals of a given area, each species should be considered as being a component part of the fauna. It is customary, however, to pass lightly over many of those whose distribution is general and to lay stress on those whose associational value is more obvious. This I think leads to an exaggerated view of the importance of particular species of more limited range. Of New England mammals the black bear is a species ranging over nearly the entire continent of North America from the highlands of northern Mexico to the Fur Countries, yet the amount

of variation it shows is relatively slight. It is an animal of high intelligence, adaptable and versatile, able to live on a varied diet of vegetable as well as animal food, factors all of which are important in permitting it to cover a wide area. The puma is an even wider-ranging mammal, extending as a species from Patagonia to southern Maine, with numerous geographic variants. In a general way its range in New England was more or less coincident with that of the white-tailed deer, on which it largely preyed. It is interesting that it closely resembles the deer in the general hue of its coat, a matter that results perhaps from similar slinking habits in a similar silvan environment.

I wish to speak especially of a certain number of New England mammals that may be ranged in pairs of more or less closely related species whose ranges in each case are practically complementary. That is, one species of each pair is in its general distribution boreal, while the other is equally austral. Two of our common squirrels illustrate this. The red squirrel (*Sciurus hudsonicus* and subspecies) is abundant and characteristic of the transcontinental spruce and pine belt from Alaska to the Atlantic; it is typically a lover of coniferous forests, and depends for a large part of its food on the seeds of various cones. In central and southern New England where hardwood forests in part replace the conifers, it depends partly on the fruits and seeds of other species, but even here is partial to clumps of pines be they ever so scattered. In contrast to this species is the gray squirrel (*Sciurus carolinensis* and races) which is typically a nut-eater, resorting to cones only in times of scarcity. Its range is chiefly southern, from Florida to central New England on the coast, though extending farther north in the interior. The two species meet within our limits, but the northward extent of the gray squirrel coincides rather closely with that of the beech-woods, the red oak and the sugar maple, all of which furnish it with staple food.

A similar complementary distribution is shown by

our two flying squirrels. One is a larger, darker animal of essentially northern distribution, found, as a species, from the forested parts of Labrador, westward to Alaska, with a number of local subspecific forms. In northern New England it is the only flying squirrel, and extends as far south as the higher country north and west of Boston, and upon the higher Alleghenies. The other is a much smaller and less darkly colored species whose range is southeastern, from Florida and eastern Texas to central New Hampshire and central Vermont. Its range is thus essentially austral, though in parts of New Hampshire, Vermont and Massachusetts the ranges of both overlap. I know of one locality in the first-named state where individuals of both species came nightly one winter to feed at the same window-shelf on nuts put out for them. We do not know, however, what actual differences in food preference each may have.

Two species of white-footed mice (*Peromyscus*) have a like relation. The northern fir and spruce forest is inhabited by a gray-furred species with a long tail and a skull differing in its proportions from that of the more southern animal. With many slightly different forms, according to local environmental conditions, the first species (*maniculatus*) is found from Labrador to central Maine on this coast, and south along the tops of the higher mountains, westward to the Pacific, from Alaska to southern California. In New England it is not found in southeastern Maine or New Hampshire, nor in Massachusetts except in the higher parts of Berkshire County. The more southern complementary species (*Peromyscus leucopus* and races) extends from Texas and Georgia to central New England and Minnesota with a few poorly marked subspecies. Where the two species meet, the more northern inhabits the cool damp spots along forest brooks, while the more southern is common in drier places, although it has invaded more or less the edge of the other species' range. The two,

although superficially much alike, are everywhere perfectly distinct.

Two species of field-mice or meadow-mice (*Microtus*) may be contrasted, though their cases are not exactly similar. One is in general more northern (*M. pennsylvanicus*), ranging as a species from Labrador to the Carolinas and westward across the northern United States to the Rocky Mountains. It inhabits grassy country and swamps, making burrows and runways. The other species is the so-called mole-mouse or pine-mouse (*Microtus* or *Pitymys pinetorum*) of the southeastern United States from Georgia and southern New England westward in bottomlands to the edge of the plains, and even into eastern Mexico. Its more subterranean habits leading to adaptive mole-like modification of the pelage together with slight but essential differences in the enamel pattern of its cheek-teeth are currently regarded as of sufficient importance to warrant its inclusion in a separate genus. The same two groups occur in the Old World, the first, as here, the more northern in its distribution.

Another genus of meadow-mice is *Synaptomys,* the lemming-mouse, which externally looks like a very short-tailed *Microtus,* but it differs widely in the minute structure of the teeth. Two groups are known, both confined apparently to North America, and now considered subgenera. The first (subgenus *Mictomys*) differs from the more typical *Synaptomys* in details of the enamel foldings, and is high northern in distribution. Various more or less nominal species are now known which, in a final estimate, will probably be referred to a single or perhaps two species with various slightly differentiated local races, extending from northern Labrador and the White Mountains of New Hampshire west to Alaska and Washington. The complementary species, *Synaptomys cooperi,* with a few slightly characterized local races, extends from Kansas to North Carolina and northward to Nova Scotia and southern Quebec, where the ranges of the two overlap, that of the more austral

species passing well into the cool northern forested country.

The case of our two lagomorphs is again in point. The varying hare (*Lepus americanus* and races) is an animal of the cool evergreen forests from Labrador to Alaska. In New England it follows south along the western highlands and in eastern Massachusetts, Rhode Island and Connecticut is very local, in our extensive white-cedar swamps. Of more southern distribution is the cotton-tail rabbit (*Sylvilagus transitionalis*), an allied but more primitive genus, an animal of more open bushy country, whose range now includes southern Maine, south-central New Hampshire and parts of Vermont. It has probably extended northward slightly in recent decades.

Two species of lynx are found in New England: the larger, more northern is the Canada lynx of the Fur Countries, formerly common in the Maine woods, probably also northern New Hampshire and Vermont. It has been much depleted in numbers with us through persistent trapping and there is much reason to suppose that its place has been largely occupied by the more southern bay lynx, whose range as a species is from Florida and northern Mexico to Nova Scotia on the Atlantic coast, and to parts of California on the western coast. The chief food of the Canada lynx is the varying hare, while that of the bay lynx includes the cotton-tail rabbit. Both form an interesting parallel, that may be further accentuated by the fact that both species of lynx are bob-tailed with long hind limbs, like the rabbits, an adaptation no doubt for quick progress in thick cover.

Our two genera of foxes may be considered here. The common red fox (*Vulpes fulva*) of the north in its various subspecies is abundant from southern Labrador to Alaska, and southward to Virginia. An allied genus, the gray fox (*Urocyon*) is typically southern, but is now found in Connecticut, parts of western Massachusetts, southern Vermont and southern New Hampshire. It has possibly pushed northward slightly in the last cen-

tury. The largest races are found in the north, with dwarfed forms extending into Central America and even to the coast of southern California.

Another couple is found in our two species of stoats or weasels. The smaller, shorter-tailed species (*Mustela cicognanii*) is abundant in the northern evergreen forests from Alaska to Labrador, southward in the east to southern Connecticut and to some of the higher Alleghenies. It becomes rare south of Massachusetts. In the north it is essentially a mouser, but is also an enemy of the chipmunk and red squirrel. Meeting the range of this species is the larger, longer-tailed New York weasel (*Mustela noveboracensis*), commoner to the south, and ranging eastward to New Brunswick and into central Maine. It is a relentless foe of the cottontail rabbit, and has perhaps extended its range slightly to the northward in the late centuries. In central and southern New England both species occur together. As if in proof of their respective origins, the more northern species invariably turns white in winter like the ermine, even in winters that, in southern New England, may be nearly snowless. The more southern species, on the other hand, although usually turning white in the northern part of its range, does not always do so, and in the south is usually brown in winter.

What then is the significance of the distribution of those species here selected for discussion? In most of the cases, the more northern of each pair has a transcontinental range, within the spruce and fir forest, whereas the more southern counterpart has a more restricted distribution, *east* of the plains, in general corresponding to the hardwood forest area. Several of the more northern species have close relatives in the northern parts of the Old World, whence they may have arrived in late Tertiary times. May it not be that the more southern complementary species, as well as others now of a more or less restricted distribution in the east, are the survivors of a still earlier invasion from Asia and had once a more extended transcontinental distribution,

but have since been driven out in the west through progressive desiccation, perhaps since Miocene times, due to the rise of the Rocky Mountain system and the consequent withdrawal of moisture from the prevailing westerly winds? Paleobotanists, reasoning from the known flora of Tertiary times, conclude that in the early Tertiary the hardwood forests, mostly of familiar genera, extended very much farther west, and that even by the Miocene, the northern hemisphere had still a largely cosmopolitan flora. Presumably the characteristic species of mammals accompanied this hardwood forest in its westward extension, but with its retreat eastward, these have been forced to give place to a different set of species, some of which, as the western chipmunks (*Eutamias*) and ground squirrels (*Citellus* and allied genera), are no doubt invaders from Asia in relatively late Tertiary times.

Another interesting point is that the exact southern limit of no two of these northern species is quite the same; nor do the northward boundaries of any two southern species exactly coincide. The explanation is, obviously, that each species has its special requirements and is limited by them. The case of our three New England moles illustrates this fact. All are distinctively of *eastern* North American distribution at the present time. The common mole (*Scalopus aquaticus*) of the south is abundant from eastern Texas and Florida northward to southern Michigan and the southern edge of Massachusetts. It is met by a northern species of a different genus, Brewer's mole (*Parascalops breweri*), which it resembles in a general way, though the two are very distinct structurally. The latter species ranges from southern Canada, south in the east to east-central Massachusetts, apparently not reaching the coast in this state. Southward it follows the Alleghenies to Georgia, at some altitude, however. The ranges do not actually overlap in New England, but there seems to be a slight hiatus between them. This brings us to a consideration of another factor that has a bearing on the distribution,

namely, the soil preference of each species, which in turn is perhaps conditioned in part by food. Thus the southern mole tunnels near the surface in light sandy soil, following this in southern New England to the base of Cape Cod and up the Connecticut Valley as far as Springfield and vicinity. Additional data are much desired as to localities in this state. In eastern Massachusetts, the gravelly range of hills stretching southwest from Manomet, near Plymouth, seems to form an effective barrier to its extent northward. The Brewer's mole, on the other hand, is a deeper burrower at times, and seems to affect much more compacted soil, sandy or even gravelly. Our third species, the star-nosed mole, is primarily a species of swamps, with partly aquatic habits. It occurs from Labrador to the Carolinas, but not very far westward.

Our two species of jumping mice—now considered generically distinct—well illustrate the difference in requirements just alluded to. The widely ranging jumping mouse (*Zapus hudsonius*) of our meadows and hay fields is almost wholly confined to grassy lowlands and open sedgy swamps. The woodland jumping mouse (*Napæozapus insignis*), on the other hand, is, as its name implies, a lover of the northern forests, seldom found more than a few yards from the banks of some little woodland stream. What the precise factors are that limit the ranges so closely are still almost unknown to us. A closely allied jumping mouse is found in the mountains of southwestern China, and indicates a general range for the group that must once have been much wider.

Of particular interest is the case of our common white-tailed deer (*Odocoileus virginianus*). In slightly differentiated races it occurs from Panama to New Brunswick, and seems to find its optimum living conditions in the north, where it grows to a large size. Less than a hundred years ago, it was practically absent from much of central and northern Maine and New Brunswick, where now it is abundant, though remains from shell

heaps indicate that it ranged normally along the sea coast to Nova Scotia, even in prehistoric times. The chief factor in permitting this extension of range is probably the extermination of its arch enemy the wolf. In deep snow with a light crust, the deer were practically at the mercy of the wolves, and in an unfavorable winter very few could have escaped at the northern edge of the species' range, for the wolves would get every one. Now, however, with the wolf quite gone, the deer easily overruns all northern New England.

Many other cases might be cited of the close dependence of species on particular combinations of factors. It is clear, however, that in any study of distribution, two main considerations stand out, namely, the past history of the species and its particular biologic requirements. These two factors are likely to be different for each species, so that it should be no source of wonder that common boundary lines can seldom be laid down as delimiting the distribution of a given number of species.

ECOLOGICAL ASPECTS OF BIRD DISTRIBUTION IN TROPICAL AFRICA

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FOR some years past I have been investigating the avifauna of the Belgian Congo, and the remarks I shall make are prompted by my attempt to divide that broad area into faunal districts, and then to correlate such subdivisions with others extending beyond the Congo borders to the remainder of the continent. I have had to reconsider the faunal areas already proposed by Wallace, Reichenow, Sharpe,[1] and several other authorities. Fortunately, their conclusions need modification only in detail. I shall concern myself rather with the causes responsible for faunal diversity, but in so short a paper

[1] *Natural Science*, Vol. III, 1893, pp. 105–107, with chart opp. p. 108.

it will not be feasible to offer lists of species of birds in justification of my course, or to sketch it in more than its rough outline. My more thorough discussion, dealing particularly with the birds of the Belgian Congo, is shortly to be published in the *Bulletin of the American Museum of Natural History.*

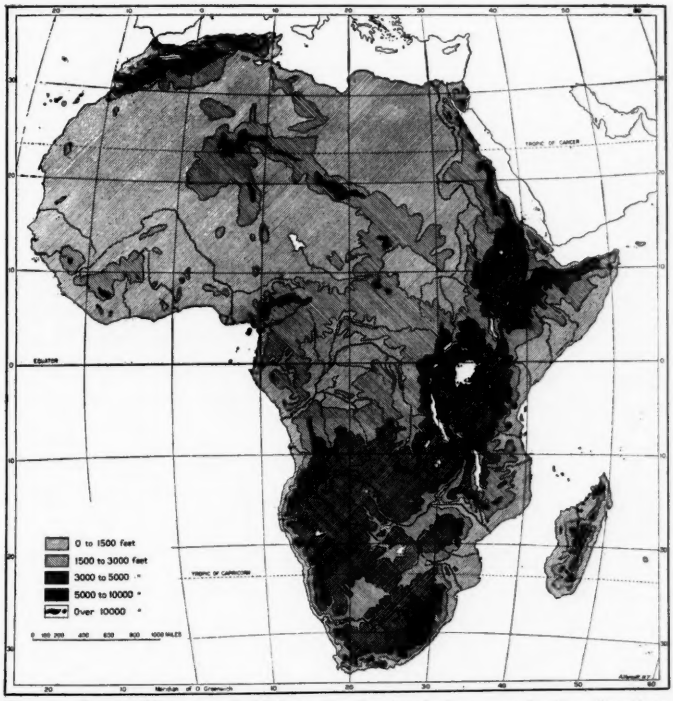

FIG. 1. Orographic map of Africa. In the tropical zone only the elevations above 5,000 feet have an important bearing on bird distribution.

The differences between the avifauna of tropical and southern Africa and that of the adjoining continents and islands are in a great measure the result of isolation by arms of the sea. But when we come to inquire into the reasons for lesser faunal areas upon the African continent, or the contrast, for example, between the faunas of the western and eastern sides of equatorial Africa, we find that the physical barriers alone are

scarcely sufficient to obviate extensive mingling of the animals. The key to an understanding of present-day bird distribution in Africa will be found in ecological conditions, especially the nature of the vegetation, which is an index of the climate.

Instead of a lofty mountain chain, like the Andes, Africa has only a broad highland extending from Abyssinia to Nyasaland, through the eastern half of the equatorial belt, and then sending a branch westward to southern Angola, while several disconnected highlands are scattered south of the Zambesi. Africa's high mountain peaks, often of volcanic origin, are isolated, and rise mostly from the eastern part of the continent, though Mt. Cameron and Clarence Peak are to be noted as exceptions.

Where the African highlands rise above 5,000 feet, and receive at the same time sufficient rainfall to support a mountain forest, they exhibit faunal peculiarities; but the number of species of birds whose distribution is thus limited is relatively small. We now know of approximately 1,050 species of birds which occur within the limits of the Belgian Congo. Out of this total, those restricted to the mountains above 5,000 feet, the Kivu volcanoes, the Ruwenzori range, and neighboring elevations, amount to only 92 species. The avifauna of the grassy highlands between 5,000 and 6,000 feet is not unlike that of steppe regions at a much lower level; it is in the mountain forests and the still higher alpine zone that the more typical mountain birds are found.

LOWLAND DISTRIBUTION

The lowlands of Africa show greater diversity in their birds than do isolated montane areas; and this lowland distribution is much less affected by variation in temperature than by that in humidity. The only barriers discernible are those of vegetation—or the lack of it—resulting from the differences in rainfall.

The life zones which may readily be distinguished at successive levels on many of the African mountains, be-

ing largely attributable to changes in temperature, have no near counterpart in the Ethiopian lowlands. Nearly the whole continent lies between the yearly isotherms of 20° Centigrade, which are often taken as the limits of the tropical zone. The northern edge of Africa is excluded from the Ethiopian Region of zoogeographers, but its faunal differences are due to isolation by the arid Sahara and past connections with Europe rather than to lowering of temperature. The southern extremity of

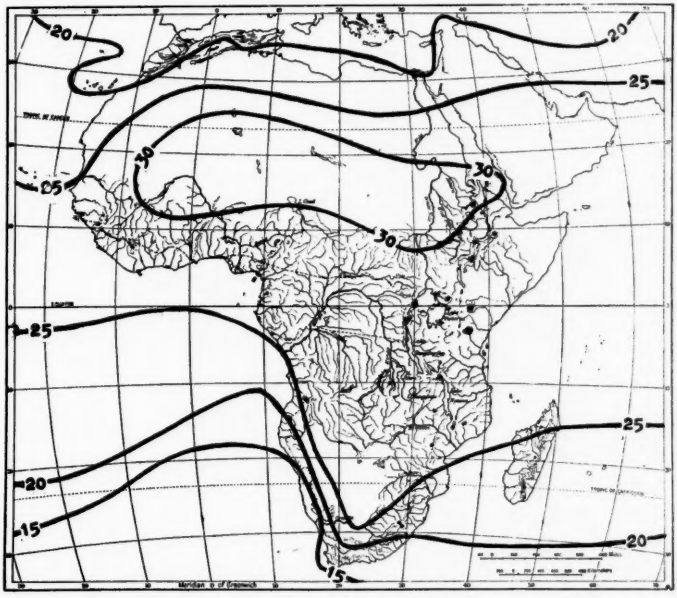

FIG. 2. Yearly isotherms in Africa (from Andree's Hand Atlas).

the continent is less distinct, speaking ornithologically, because it is not so completely cut off by desert.

In my work upon the distribution of birds in the Congo, I was early impressed by the general agreement in dispersal of the bird communities with corresponding plant associations. Fortunately I made the acquaintance in Africa of Dr. Joseph Bequaert, then on a botanical mission for the Congo Museum; and for some

years I have been able to compare notes with him, and secure information as to plant distribution.

The whole question of plant and bird distribution in Africa, particularly in the lowlands, goes back to the distribution and abundance of rains. If we examine Knox's rainfall map [2] we find the annual rainfall varying from next to nothing in some of the desert regions

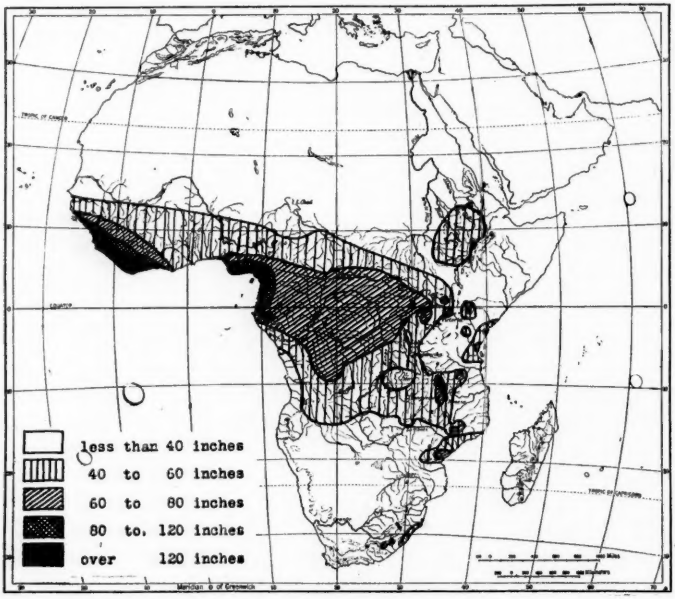

FIG. 3. Total annual rainfall in Continental Africa (after Knox). Note how many points of similarity exist between this map and the avifaunal map in Fig. 11. The seasonal distribution of the rains is next in importance to their total amount.

(both north and south of the equator) to over 160 inches along considerable stretches of the West African coast. On the slopes of Mt. Cameroon it attains 412 inches. Wherever the rains exceed 60 inches annually, the country is apt to be covered with dense tropical forest, although the seasonal distribution of the rains often holds the balance of power.

In Sierra Leone, where there is a dry season of four

[2] "The Climate of the Continent of Africa," 1911, Pl. I.

months, a total annual rainfall of 170 inches does not suffice for a continuous forest growth. Wooded patches are intercepted by grasslands. In parts of the Upper Congo, on the other hand, where the rains scarcely reach 65 inches, a superb, unbroken forest persists because there is seldom a month without rains. Despite the drier nature of eastern equatorial Africa, there are spots with heavy rainfall, due to local topography. They likewise support heavy forest, but more often it is of montane type.

Going from the barren rainless areas of Africa toward the equatorial forests, one finds first grassy steppes, with few trees, widely scattered, and at length a savanna country often bountifully studded with trees, or even wooded. But everywhere there is withal a luxuriant growth of grass beneath the trees, save in

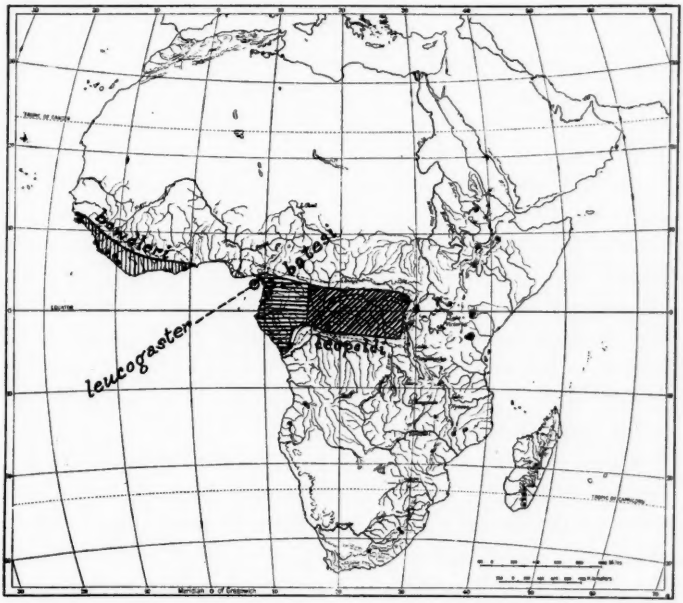

FIG. 4. Distribution of *Corythornis leucogaster*, a small African kingfisher living along brooks only in the dense forest. Four geographic races are recognizable, resulting from partial isolation. They differ from each other in details of color pattern and in size of bill.

especially moist spots like ravines and river-bottoms, which have gallery-forests resembling strips of the equatorial rain-forest. Here the trees owe their luxuriance to ground water. The entire equatorial forest belt is characterized by the extreme scarcity of grasses.

It is through these different types of vegetation that the rainfall determines the distribution of birds. For instance, the forests in many parts of Africa are so extensive that they exclude wholly, from wide areas of the continent, many typical Ethiopian birds, not only such as rely upon grasses for their food, but even fruit-eaters like the colies. The contrasts in preferences as to vegetation are of such weight that we may speak of the African avifauna, with the exception of littoral species, as divisible into forest, savanna, montane, and desert associations. Even the waterfowl show distinct preferences for forest or open country. Hartlaub's duck (*Pteronetta hartlaubi*) is confined to the wooded streams of the West African subregion; whereas the Egyptian goose, like the spur-winged, shuns all but the very broadest rivers of the forest country, for they prefer those of savannas and steppes.

Certain species of birds, nevertheless, are often stated to occupy practically the whole Ethiopian region. In many instances this is erroneous; in the few where it is approximately true, there is a good ecological reason. The hawk, *Kaupifalco monogrammica,* for instance, is able to find subsistence in the clearings of the equatorial forest, whereas in the savannas it will generally be found only where the trees grow thickest, as along the borders of gallery-forests.

To one who studies the birds of the forest at first hand it will be further evident that there is a second-growth association of birds, distinct from those of the virgin forest. Mr. William Beebe [3] has already called attention to this in British Guiana and Mr. G. L. Bates [4] in the Cameroon. Its importance is enhanced by the waste-

[3] "Tropical Wild Life in British Guiana," 1917, pp. 60–61.

[4] *Ibis,* 1904, pp. 593–4; 1909, p. 5.

ful manner in which the African native is continually cutting down the virgin forest to establish farms for his plantains, which so soon impoverish the soil that the villages are ever being displaced. The rapid-growing woods, famed in stories of travel, are second-growth, the trees of which have soft, light wood, and never attain the majestic size of the slow-growing virgin forest.

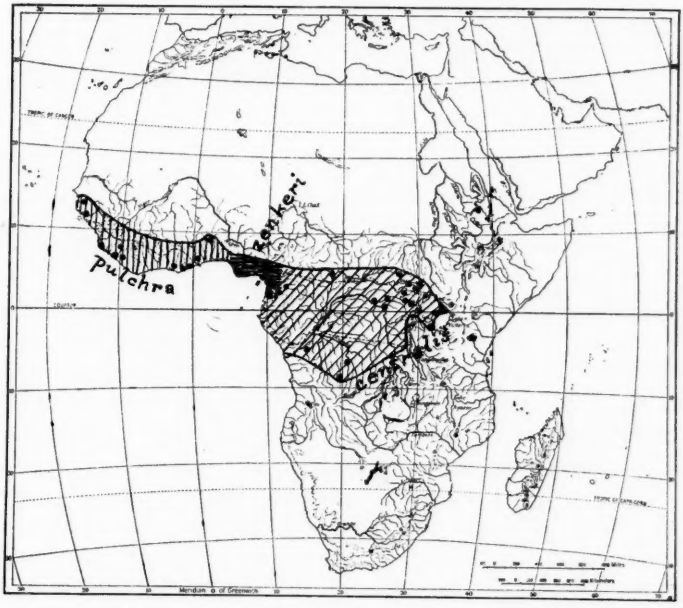

FIG. 5. Distribution of *Sarothrura pulchra*, a small rail frequenting the banks of wooded streams, and extending its range out into the gallery-forests of the Guinean savannas.

They favor reforestation, however, by casting shade sufficient to exclude nearly all grasses. Inasmuch as the natives frequently neglect to cut down all the mature forest trees in their plantations, it is a common thing to find extensive tracts of second-growth woods, overtopped by a sprinkling of true forest trees, yet the birds characteristic of the lower levels in virgin forest will be sparingly represented there. I think I do not exagger-

FIG. 6. Diagram to illustrate the succession of forest vegetation after clearing by natives. Note the height of the virgin-forest trees, as compared with the second growth, and the denser lower vegetation in the latter.

ate in estimating the period required for complete reforestation at well-nigh eighty years.

The savannas of Africa vary exceedingly in the abundance of trees and the height of the grass. They occupy the regions where the total annual rainfall is less than 60 inches, or where there is a dry season of two months or more, if not—as in eastern equatorial Africa —two short dry seasons. Many resemblances are seen between the birds of the savannas north and south of the Congo forest; but so often are they specifically different that they seem to indicate more complete segregation in the past, perhaps by the extension of the forest all across the continent. The savannas harbor the horned guinea-fowls (*Numida*), the bustards, the colies, hoopoes, and many other genera of the most characteristic Ethiopian birds.

The avifauna of the deserts is generally more restricted as to species than that of the humid regions, and is characterized especially by sand-grouse, coursers and larks. The distribution of the various forms of ostrich is readily understood if we keep in mind the preference of the group for steppes bordering on the deserts. The four forms commonly recognized in Africa

by systematists are characteristic of as many arid regions of the continent, and are kept apart by the more luxuriant vegetation which intervenes.

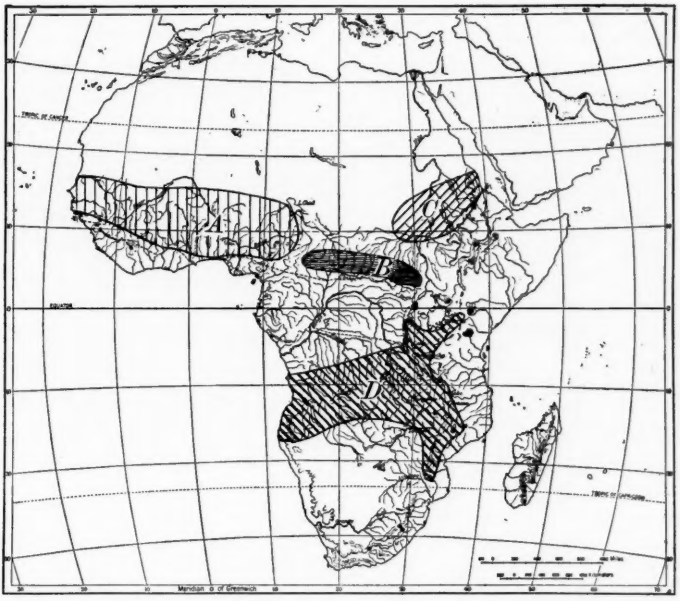

FIG. 7. Distribution of the races of *Steganura aucupum*, the broad-feathered Paradise Whydah. A, *S. a. aucupum;* B, *S. a. interjecta;* C, *S. a. nilotica;* D, *S. a. obtusa.* Such a dispersal is characteristic of many groups of savanna birds, which are segregated by the rain-forest of the Cameroon and Congo.

ALTITUDINAL LIFE ZONES

Life zones on the African mountains will be found best marked on those peaks which rise within a few degrees of the equator, and therefore are more favored with rains. Between 5,000 and 10,000 feet, on the mountains of the eastern Congo, there is often a complete girdle of mountain- or cloud-forest. This is the habitat of the majority of distinctive mountain birds, which differ specifically in most cases from those of the adjoining lowlands, but are occasionally related to lowland forms in the cooler parts of South Africa.

The upper half of the mountain-forest, in eastern

Africa, is frequently composed of bamboos (*Arundinaria alpina*). Perhaps because of a mingling of vegetation, the bamboo zone is inhabited by much the same birds as the ordinary mountain-forest; so that I am inclined to unite the two floral zones, in so far as birds are concerned, into one subtropical or mountain-forest zone. Above the bamboos, from about 10,000 to 12,500 feet, there is often a zone of tree-heaths, *Erica arborea* on Mt. Ruwenzori, but an *Ericinella* on many of the East African mountains. On some of the Kivu volcanoes there are other large trees at this level, which should correspond to the temperate life zone of the Andes, which Dr. Chapman finds so important in the distribution of South American birds. On the African mountains it is poor in birds, and has almost nothing truly characteristic. I would attribute this to lack of communication with mountains of corresponding height to the north and south, and the small size of the temperate areas themselves.

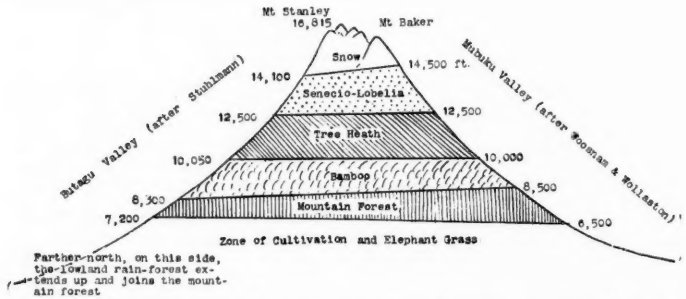

FIG. 8. Diagram of the floral zones on Mount Ruwenzori, as seen from the south. The distribution of its birds depends upon the zones of vegetation, but it seems wiser to unite the mountain-forest and bamboo zones into a single subtropical faunal zone, and the tree-heath and Senecio zones into an alpine faunal zone.

Above the heath zone is an alpine zone which is not exactly treeless, for the vegetation includes giant arborescent groundsels and tall lobelias, which dwindle away as the snowline is approached. This cold, inhospitable part of the high mountains has few birds. On Mt. Ruwenzori the British Museum Expedition found

only 7 species of birds dwelling in it.[5] To the tall flowering spikes of the lobelias come long-tailed sunbirds, of the species *Nectarinia johnstoni,* which is represented by four races on different mountains of East Africa.

If the heath zone of Ruwenzori be included in the alpine zone, as seems advisable, the whole avifauna will amount to about 15 species of which only four have not been found below the level of the tree-heaths.

Explanation of Present Montane Distribution

The resemblances between birds of the high mountains of Africa extend in a number of cases even to Mt. Cameroon and the peak on the Island of Fernando Po. A trogon of the mountain-forest, *Heterotrogon vittatus,* is found there as well as in East Africa, and shows only

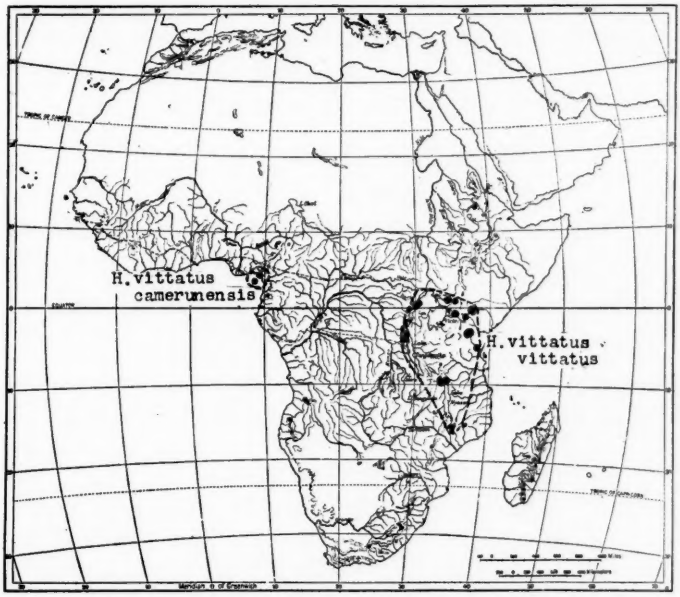

Fig. 9. Distribution of *Heterotrogon vittatus,* a Trogon restricted to mountain-forests. All the central Congo basin, though forested, is too low to harbor it, and this isolation is responsible for the slight differences which have arisen between the eastern and western subspecies.

[5] R. B. Woosnam, *Trans. Zool. Soc.,* London, 1909–1910, Vol. XIX, pp. 21–23.

a slight subspecific difference. There are parallel similarities in plants, and the botanist Mildbraed,[6] speaking from a thorough acquaintance with field conditions, rejects an explanation based upon chance distribution of seeds by winds or migratory birds. More probably there were changes of topography and climate in the past which permitted extension of the mountain floral zones, thus connecting some of the montane areas now widely separated.

Still more widespread changes in rainfall must be invoked to explain the resemblances between the avian and mammalian faunas of West Africa and the forested parts of the Oriental region. We believe that in Miocene time there was a belt of tropical rain-forest stretching most of the way between India and Africa, where drought now prevails and has long isolated the two forest faunas. Such changes in the vegetation are of more importance for the dispersal of birds than mere land connections would be, across the Red and Mediterranean Seas.

BIRD MIGRATION AND VEGETATION

In our temperate-zone home, we are accustomed to see birds wander far more widely—as soon as the breeding season is past—than species of the tropics are apt to do. The rigors of our changing seasons necessitate migration. Close to the equator, and especially in a rain-forest, no such incentive exists, and all the small birds are extremely sedentary. But in Africa, as soon as we go a little to the north or south, where an annual dry season parches the countryside, we find seasonal movements of birds by which they tend to adjust themselves to changing conditions of humidity and food-supply. Many move from the drier Sudan, for instance, southward to the savannas closer to the Congo forest, a journey of some few hundred miles. Others cross the humid equatorial belt and find an advantage in the reversed

[6] "Wiss. Erg. Deutsch. Zentr. Afr. Exp. 1907–8," Mecklenburg, 1914, II, p. 689.

season on the opposite side of the line. Abdim's stork and the pennant-winged nightjar are examples of the latter class.[7] They do not tarry long in crossing the Congo forest, but in East Africa, where there are grassy stretches on the equator, they may stop as well in the intermediate latitudes.

The effect of the general type of vegetation is again evident in the migrations of Ethiopian birds. It may also be noted in the winter ranges of many Palæarctic birds which invade Africa annually.

The equatorial forest is a barrier which fixes the

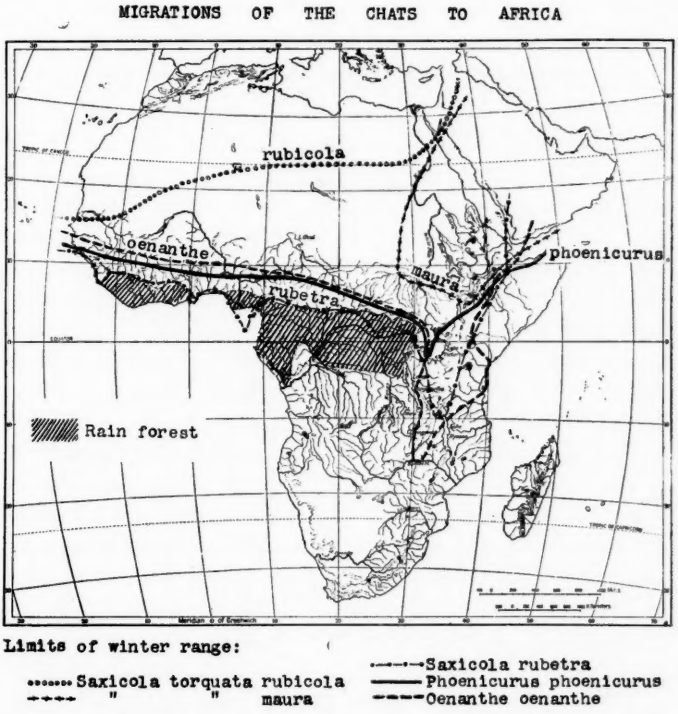

FIG. 10. Migration of the Palæarctic chats to Africa. The lines showing the southern limits of the whinchat, the redstart and the wheatear are clearly fixed by the great lowland rain-forest of western and central Africa, whereas in east Africa, three of the forms go farther south.

[7] Chapin, James P., *Amer. Mus. Journal*, 1916, pp. 540–545.

southern limit of many species, such as the nightingale, the redstart and the wryneck. Inasmuch as it is broken in East Africa, many species find their way farther south on that side of the continent, some reaching Cape Colony without having to cross the forest belt. Others which extend their migrations to South Africa travel largely along the seacoast (*e.g.*, many shorebirds), or some boldly cross the Congo forest, where they are seen regularly in the clearings (*e.g.*, red-backed shrike, lesser gray shrike, swallow, roller). Such migrants from Eurasia are never seen within the shade of the rain-forest itself.

AVIFAUNAL MAP OF AFRICA

With Dr. Bequaert's assistance I had divided the territory of the Belgian Congo into eight faunal areas, without counting the further subdivision of the humid montane area into altitudinal life zones. In compiling a complete list of the avifauna of the Congo I discovered that the ranges of the various species and races could be expressed succinctly by reference to these areas, while at the same time they could be readily characterized in general botanical terms.

With this encouragement I tried to extend my avifaunal map to cover the whole continent. My tentative map differs in certain minor points from any of the preceding, though agreeing with them all in the recognition of the faunal importance of "West Africa." This I make one of the two subregions of the Ethiopian region. The avifauna of Madagascar is distinct enough to merit regional separation from continental Africa.

The western fauna owes its distinctness to ecological or climatic conditions, as comparison with the rainfall map of Africa will prove. It is the principal area of more than 60 inches annual rainfall; and I am led to believe—from its dependence on the most fundamental movements in the atmosphere—that such a humid area near the equator is of vast antiquity. Its equable climate and luxuriant vegetation have proved a refuge for

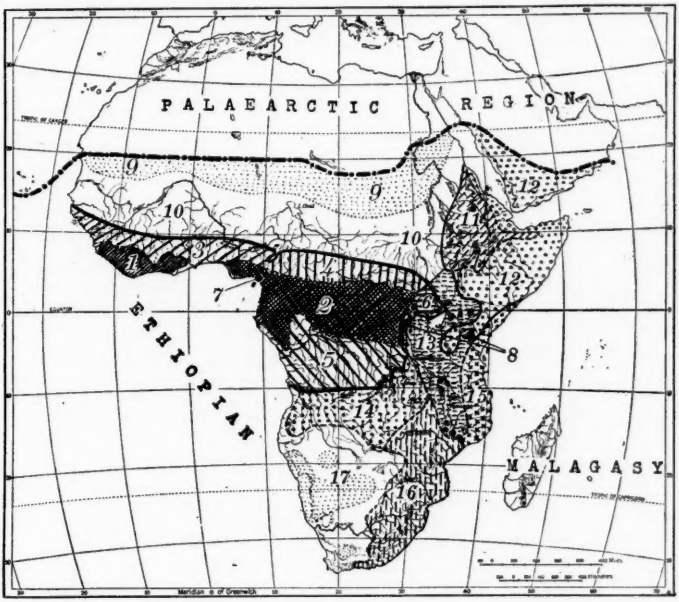

FIG. 11. Avifaunal map of tropical and southern Africa. The Ethiopian region, from which I exclude Madagascar, is divided into two subregions, and these in turn into six provinces composed of seventeen minor districts.

many rather generalized groups of birds, which may have extended farther northward in past geological ages with a more humid climate.

We must not think of the boundary assigned to this subregion as a mountainous ridge offering a barrier to bird travel. Herbert Lang and I spent two years close to the northeastern part of the boundary, in the upper Uelle river district, and found that many species of birds make annual migrations, *en masse,* across this very line. The boundary simply marks the extreme limits of distribution of many members of the forest fauna, the gray parrot, the great blue plantain-eater, and the chimpanzee, because at this point the gallery-forests terminate, due to reduced rainfall during a considerable part of the year. The principal faunal bound-

ary in Africa (for birds and mammals) is ecological, resulting directly from climate.

The influence of topography is more apparent in eastern Africa, because of the effect of elevation upon air-currents and precipitation. Within 5 degrees of the equator elevations over 5,000 or 6,000 feet are very apt to be forest-clad. Yet in 12 degrees south latitude, in the Katanga, at the same altitude the effect is reversed, for the dense savanna woods of lower levels give way to open highland prairies with only occasional gallery-forests along the headwaters of some of the streams. This is attributable partly to the long dry season, of 4 or 5 months, and partly to the poor nature of the soil. Latitude is of more weight in determining humidity than in its effect upon temperature—till we reach the limit of the tropical zone.

Another sharp line of faunal demarcation in Africa is that of the border of the equatorial rain-forest. I mean the line where savannas begin to interrupt the forest. This is the "inner" limit of numbers of savanna forms, even though a few may penetrate to isolated artificial clearings in the forest; and beyond it, too, the forest fauna undergoes rapid diminution, being hidden for the most part in narrow gallery-forests.

Neave [8] has called attention to a marked change in the bird fauna as one rises from the lower Zambesi valley to the higher levels of northern Rhodesia. The change is not due to altitude alone, for many of the birds of northern Rhodesia and the Katanga are found elsewhere at no more than 1,500 feet above sea level.

In East Africa the striking difference between the Tsavo desert district and the highland veldt to the westward has sometimes been spoken of as though due to altitude. This is probably only involved in so far as it affects rainfall.

In South Africa the distinctness of the eastern and western avifaunas is clearly a matter of rainfall and its

[8] *Geographical Journal*, 1910, Vol. XXXV, pp. 132–144 and map opp. p. 224.

effect upon the vegetation.[9] North of the equatorial forest we find that there is a similar line of demarcation; but it runs in another direction, from west to east, in a remarkable manner, from Senegal to the Upper Nile. When we follow the long, narrow ranges of many species of birds, from the region of the Gambia across the highlands of Fouta Djalon, down into the low valley of the Niger and up along the Ubangi to the Congo-Nile divide, we can not fail to recognize the unimportance of variations in altitude below 5,000 feet, and the predominant influence of rainfall, as reflected in the vegetation.

Going a little farther east, we may note that the differences in avifauna and flora between Abyssinia and Somaliland are clearly correlated with rainfall (see map), and only have to do with altitude in so far as this determines the amount of precipitation.

Nature of Faunal Boundaries

A word of apology may be necessary for my arbitrary drawing of faunal lines. I know of no better method of calling attention to the differences one would observe in the bird population on going from one part of the continent of Africa to another. I willingly admit that the change is far more gradual than a hard black line would indicate. A broader band of color, fading imperceptibly toward its edges, might carry a truer picture of actual changes. Many species will boldly transgress the limits I have tried seemingly to erect. What I really hold is that there are areas with characteristic complexes or associations of species; and they might be further subdivided, if we cared to, according to more local habitats, depending on the particular haunts of each species—and in this no two are exactly the same.

The travelling ornithologist, as he goes from the Guinean savannas into the rain-forest—for instance—listens to unfamiliar bird voices as he walks along the heavily shaded wood paths. For the first few days prac-

[9] The wooded coast of Natal is perhaps worthy of separation as another district, making three in all, for South Africa.

tically all of them are strange to his ears. The grass-dwelling birds have been left behind, and a new fauna awaits his investigation.

SUMMARY

The general conclusion to be drawn from my map is that although temperature may be a distributional factor of weight, it acts most visibly along certain critical lines, as that, for instance, where occasional frosts first occur. Such a line may be a rough boundary for the tropical life zone, altitudinally as well as on the north and south. Other similar lines are found as the subarctic region is reached, and on mountains, where trees disappear.

Within the limits of the tropical zone, temperature alone has no further effect on distribution; humidity now becomes the predominating factor. Its effect upon bird distribution is produced through the development or the paucity of vegetation, the relation between plant associations and their bird inhabitants being particularly close in the African tropics. Avifaunal lines of demarcation are never more sharply defined than the changes in composition and habit of the vegetation. A difference in plant associations may also serve as an isolating factor, just as often as altitude. More than likely, the isolation by altitude, indeed, is again secured through changes of the montane plant-formations.

Subdivisions of the Ethiopian Region

I. West African Subregion.
  A. Guinean Forest Province.
    1. Upper Guinea Forest District.
    2. Lower Guinea Forest District.
  B. Guinean Savanna Province.
    3. Upper Guinea Savanna District.
    4. Ubangi Savanna District.
    5. Southern Congo Savanna District.
    6. Uganda-Unyoro Savanna District.
II. East and South African Subregion.
  C. Humid Montane Province.
    7. Cameroon Montane District.
    8. Eastern Montane District.
  D. Sudanese Province.
    9. Sudanese Arid District.
    10. Sudanese Savanna District.

E. Northeast African Province.
11. Abyssinian Highland District.
12. Somali Arid District (incl. S. Arabia).
F. Eastern and Southern Province.
13. East African Highland District.
14. Angolan Highland District.
15. East African Lowland District.
16. Southeast Veldt District.
17. Southwest Arid District.

REPTILES IN THE EAST AND WEST INDIES—AND SOME DIGRESSION

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THE more nearly complete knowledge of the fauna of the earth which has resulted from the intensive collecting of the last few years has inevitably forced changes in zoogeographic concepts which were previously held. Wallace's line has gone and the North American Life Zones, so favorably discussed by writers only a few years ago, are now definable in a small way only. Thus, as Dunn has put it, where zonal lines coincide with physiographic barriers there is a noticeable change of fauna within a few miles and the result is a visible and definable limit. Lutz's paper on "Geographic Averages" served some useful purpose in emphasizing the unsatisfactory state of our terminology for faunal divisions within the greater land masses. We can not see, however, that he has offered a happy issue out of this affliction. None of the areas previously defined has really described the distribution of more than a very few forms and these only in vague terms. Dunn has made a suggestion pregnant with possibilities of future usefulness, viz., to use the "New Geography" and he has already used the "Physiographic Divisions of the United States," prepared by Fenneman, with real ease and comfort. When such divisions are defined for the other continents, then most, if not essentially all, of our present difficulties will cease to exist. In the areas which I have chosen to remark upon there are no zones to be named, for the East and West Indies are made

up of broken lines of islands and the adjacent elements of each chain differ in their faunas one from the other in moderate degree. In the East Indies there is no Wallace's line, no Weber's line and no sharp boundary of any sort which defines the ranges of more than a few species. Java once was thought to have had a separate connection with the Malay Peninsula independent of that which Sumatra and Borneo had, but more skillful collecting in this island has changed this concept and now we know that Java had just the fauna to which its geographic history and position entitles it; namely, a purely Malayan fauna rather depauperate in proportion to its distance from the mainland and its lesser area. Other factors such as climate, rainfall and accessibility, being equal, the larger the island the greater the number of species to be found there and *vice versa.* In the East Indies in proportion as obviously continental types grow fewer, others derived from Australia make their appearance, so that in Lombok there are many species of Malay origin and a few of Australian, while in Ceram or Halmahera the exact reverse is true. Thus the whole central portion of Insulindia is in reality a great transition zone. What makes this contrast striking is the fact that Asiatic and Australian species are so different in facies and are so easily recognized. The many survivors of the early types which now we call Australian species have filtered back toward the mainland as various foldings and thrusts up and down have brought various islands into temporary union for greater or lesser periods of time. That the Australian types in Celebes, for instance, are reentrants and not survivors is reasonably certain, we believe. Celebes, nevertheless, has an obviously "continental" fauna by all tests and still is not a "continental" island oceanographically and the proportion of Australian species is small but conspicuous. The condition seen in Celebes is the strongest single argument against the tenets of those who maintain that flotsam and jetsam are sufficient to account for the population of these islands. We have discussed fortuitous

dispersal so fully elsewhere that there is no occasion to expand on this theme at present.

How, then, after these digressions, does the distribution of East and West Indian reptiles compare? Are conditions similar? Similar in part they certainly are, geographically. In both cases a long series of tropical islands stretch out to form a giant set of stepping stones between two continents. But in the case of Australia we deal with an island, very long isolated, while South America, greatly modified from ancient Gondwana land, is connected by Panama with Central America. South American species are far less conspicuously different from Central American than Australian are from Asiatic, for there has been less isolation to permit of change.

In the East the mainland agamids wane and but few reach Papua while the Australian skinks abound in Papua and the Moluccas and dwindle in numbers in the greater Sunda Isles. Respecting the East Indies we instinctively illustrate degree of difference by citing the distribution of *families,* whereas in the West Indies we must discuss *genera.* Thus the Central American Bufos reach out through Cuba and Haiti to little Virgin Gorda. Gymnophthalmus, Centropyx and Scolecosaurus push into the Lesser Antilles from the Guianas. But the greater part of the essentially Antillean genera range throughout the whole chain and are found on every island, islet or even rock which can support life, and this most significant homogeneity of the fauna is here the paramount argument against fortuitous dispersal. The fact that a single genus ranges all through the islands, however, is no certain proof of derivation from one mainland source only, for in the case of Ameiva and Anolis, for example, it is possible to identify groups of species within the genus, inhabiting adjacent islands, and which have come in from the opposite ends of the island chain.

A moment to compare the facies of the faunas is well

spent, too. Over much of Indonesia the skinks are dominant, successful types, arboreal, terrestrial, subterranean—even semi-aquatic. In the West Indies they are on the verge of complete disappearance. Species occur on many islands but all are on the verge of extinction. In the East Indies the Agamidæ, while conspicuous in the greater Sunda group, are not preeminently the dominant family anywhere. In the West Indies the cognate family of Iguanidæ are enormously successful. Anoles in Jamaica swarm as no lizard swarms anywhere except Lygosomas in Papua. The bold semipredaceous Varanids of the East Indies have no counterparts in the West, their place being taken by the Ameivas belonging to a family (Teiidæ) really cognate with the old world Lacertidæ, a family which has almost no hold in Eastern Asia.

Such illustrations might be multiplied but to no useful purpose.

The East Indies illustrate, on a vast scale, not only in space but in geologic time, what the Antilles recapitulate.

We may sum up by saying that distributional conditions in the West Indies are the counterpart of those in the East but differ in being in all respects lesser in degree. Their fauna occupies less area, has existed in isolation for a far shorter period of geologic time and therefore shows less taxonomic differentiation. The points of similarity are: the mixed fauna derived from two opposite sources, the relatively homogeneous fauna of contiguous islands and groups of islands, showing that the great bulk of the species involved have been derived as a result of changes of the relation of land and sea level, which have put the islands into transitory union. In both areas the waif species which have been carried about fortuitously, and there are inevitably such, can be easily recognized.

THE GEOGRAPHICAL DISTRIBUTION OF AMPHIBIANS

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IN presenting for your consideration the geographical distribution of Amphibians I have been guided in my choice of examples by their bearing on two of the more recent theories, namely, the theory of dispersal as set forth by W. D. Matthew in 1915 in his "Climate and Evolution," and the "Age and Area" hypothesis of J. C. Willis as proposed in papers from 1906 on, and restated in full in 1921.

The theses of Matthew which shall hereinafter be examined are stated by himself as follows:

1. Secular climatic change has been an important factor in the evolution of land vertebrates and the principal known cause of their present distribution.

2. The principal lines of migration in later geological epochs have been radial from Holarctic centers of dispersal.

3. The geographic changes required to explain the present distribution of land vertebrates are not extensive and for the most part do not affect the permanence of the oceans as defined by the continental shelf.

4. The theories of alternations of moist and uniform with arid and zonal climates, as elaborated by Chamberlin, are in exact accord with the course of evolution of land vertebrates, when interpreted with due allowance for the probable gaps in the record.

5. The numerous hypothetical land bridges in temperate, tropical, and southern regions, connecting continents now separated by deep oceans, which have been advocated by various authors, are improbable and unnecessary to explain geographic distribution. On the contrary, the known facts point distinctly to a general permanency of continental outlines during the later epochs of geologic time, provided that due allowance be made for the known or probable gaps in our knowledge.

6. Whatever agencies may be assigned as the cause of evolution of a race, it should be at first more progressive at its point of original dispersal, and it will continue this progress at that point in response to whatever stimulus caused it and spread out in successive waves of migration, each wave a stage higher than the previous one. At any

one time, therefore, the most advanced stages should be nearest the center of dispersal, the most conservative stages farthest from it.

It seems evident that no matter where the primitive or the advanced forms of a group are found the center of dispersal of that group should be the geometric center of the group range; or better, the geographic center, by which is meant the center of available migration routes. This idea is not definitely stated by Matthew, but it underlies his whole conception of radial migration from Holarctic centers, for granted continental permanence, the southern continents are radial to the northern land mass.

Let us now examine the distribution of Amphibian groups.

The blind, burrowing Cœcilians are Tropicopolitan. The geographic center of the Tropics is the northern land mass. The Cœcilians have reached their present ranges either by a process of retreat from a more continuous northern range, or else, by a perfectly gratuitous assumption of tremendous changes in the earth's surface, they have crossed from Africa to South America, and from Africa to India.

The *Salientia* have been examined recently by Noble, and I follow his classification.

The *Pipidæ* form a primitive family and they are restricted to South Africa and to northern South America. This distribution may be contrasted with that of a modern family, the *Ranidæ,* which occupies the whole northern hemisphere, as well as Africa, India, Malaysia and Papua, but barely reaches Australia and South America. These two families offer perfect examples of the distribution of a primitive and of a modern group as postulated by Matthew.

Several families of *Salientia,* while world-wide or nearly so, are mainly developed in the southern continents. Such are the *Bufonidæ,* the *Hylidæ,* and the *Brevicipitidæ.* The distribution of these groups has

often been held to indicate former direct connection between the southern continents, an hypothesis involving vast changes in continental outline. But no genera of Bufonids are common to South America and to Australia, none to Africa and to Australia, *Bufo* alone is common to Africa and to South America, while two genera besides *Bufo* are common to Africa and to Indo-Malaysia. The best explanation here is dispersal from a northern center. Similarly, *Hyla* is the only genus of *Hylidæ* common to South America and to any of the other southern continents, and it, as does *Bufo,* has a wide northern range. Among the *Brevicipitidæ* one genus is found both in Africa and in the East Indies, none of the other genera being common to any two of the southern regions. These two cases, like that of the *Bufonidæ,* may be explained by Matthew's theory, which involves connections only in the north between the northern continents, and hence calls for no great changes in continents or in oceans.

The *Pelobatidæ* are mainly developed in the Indo-Malay region, but some forms are found in Europe and in North America. This is surely a dispersal from a northern center, the peculiarity being that while the *Pelobatidæ* are considered a rather primitive family, they have not spread so far to the south as have the less primitive Bufonids and Hylids.

A similar anomaly, from the standpoint of Matthew's hypothesis, is presented by the most primitive family of Salientians, the *Discoglossidæ* (which alone possess ribs). Their range extends, with some breaks, across Eurasia, two species are found in New Zealand, and one in the State of Washington. This discontinuity gives evidence of vast former range and of great antiquity. No other Amphibian has reached New Zealand. But there is no lack of forms in the northern land mass.

Furthermore a modern family, the *Brachycephalidæ,* is confined to South and Middle America, and supposed to have arisen there from Bufonids.

It is clear that so far Matthew's theory is a fair means of accounting for the discontinuous distribution of southern groups; but the primitive groups are not always at the periphery; nor is it impossible for new groups to arise in the South.

The distribution of Salamanders has little bearing on the problem of northern origin, for they are almost confined to the north. One case, however, has been used as a basis for a land bridge between southern Europe and the West Indies. I allude to the supposed relationship between the Plethodont salamanders of Central America, Haiti and Italy. There is actually no close relationship between the animals of Italy and those of Central America. The Haitian salamander is either mythical or related to a Central American form. The most startling zoogeographical discovery made in the United States since Stejneger announced the finding of a Discoglossoid toad in the Olympic mountains was that of *Spelerpes platycephalus* in the Yosemite by Camp. This animal is almost identical with the Plethodont of Sardinia. So link by link the chain of argument whereby salamander distribution supported Archatlantis is broken.

The distribution of the genus *Triturus* of the family *Salamandridæ* affords an interesting example of dispersal as postulated by Matthew. This group occurs throughout Eurasia. Three species in the eastern United States are closely related to some forms of Europe, and the form of the Pacific Coast is allied to a Chinese species. The center of the group range is Europe, and judging from the relationships of the American species, this is also the center of dispersal. But besides this the group has characters whereby the primitive and specialized members can be distinguished. Sexual dimorphism can not be considered primitive, while a bony temporal arch may well be an archaic character. If we consider the distribution of these two characters in *Triturus,* the extreme sexual dimorphism is found in

Europe, dying away in eastern North America, and in Asia and western North America. The bony temporal arch is least developed in Europe, most in Asia and in America. Thus the primitive members are found at the periphery and the specialized members at the center which had been previously determined by two other lines of evidence.

The results just obtained are supported by the distribution of two still more primitve genera of the same group, *Pleurodeles* and *Tylototriton*. These range to the south of *Triturus; Pleurodeles* in Spain and in Africa as far south as French Guinea on the west coast, and *Tylototriton* in the Eastern Himalayas, Yunnan and Burma, and the Riu Kiu Islands.

The largest family of salamanders, the *Plethodontidæ*, has in many ways the most interesting distribution. Although probably the most modern group of Urodeles, it is of no mean age, as is attested by *Ensatina platensis* of Uruguay which is almost indistinguishable from *Ensatina croceater* of California. It is hard to believe that this genus can be of less than Miocene age. *Hydromantes platycephalus* of California, which has as its very close ally *Hydromantes genei* of Sardinia, affords another suggestion as to the antiquity of Plethodont genera.

The family is an eminently natural group, all lungless, mainly developed in North America, with four species in South America and two in Europe.

Lunglessness in salamanders seems theoretically and actually correlated with mountain brook life. Theoretically because the lungs of salamanders are largely hydrostatic in function, and because such hydrostatic organs would put the animal at a disadvantage in a swift current where the mode of progression is crawling on the bottom. Actually because a Hynobiid, an Ambystomid, and six Salamandrids are independently undergoing lung reduction, and are all mountain brook animals. It seems reasonable to conclude that the family

Plethodontidæ originated (took on its family characters) in a mountain region.

The problem before us is to determine this region of origin, the center of dispersal, which must have been mountainous. The geometrical or geographical center of the group range is the eastern United States. In the eastern United States and there only are found at present: The most primitive forms; all the groups of the family; all the forms now living in mountain brooks.

The original mountain-brook habitat has been largely abandoned, and many members of the family are now terrestrial. Such terrestrial forms, all lungless, are found throughout the range of the family. The assumption of this terrestrial mode of life was a necessary preliminary to migration out from a mountain region.

All this leads to one conclusion: that the *Plethodontidæ* originated in and have dispersed from the mountains of the eastern United States, in a word from Appalachia. We have arrived at this result irrespective of the fact that the primitive forms are at present restricted to Appalachia, by arguments from the center of the range, from the origin in mountain brooks (the anatomy), and from the present position of the mountain-brook forms (the ecology). Why does this result differ from Matthew's theory? Because Appalachia is an old and a conservative region, while the radial migration of his hypothesis is caused by changing conditions at the center. On the contrary, in Appalachia there have been mountains since the close of the Paleozoic; a climate now the most humid in the East; formerly not less humid, since the uplifting of three mountain ranges to the west, and the filling in of the Mississippi Embayment can only have decreased the rainfall. Therefore, in this most stable of regions there has been no such cyclic swing of change as has sent out incessantly higher and higher types from the northern hemisphere.

To sum up: The distribution of Amphibians offers as

a critique to Matthew's "Climate and Evolution" the following:

All amphibian distribution can be explained without recourse to land bridges save connections in the north between the northern land masses.

The primitive forms are not always at the periphery, although they are often found there, but may be found at the center.

The center of dispersal is best determined by the geographic center of the group range.

One family, modern and progressive, seems to have arisen fairly recently in South America.

The Age and Area hypothesis of Willis maintains that the older a genus the wider will be its range, and the greater its number of species, also that the older a species the wider its range.

From a practical standpoint the use of range to determine age is open to several objections:

There is no evidence of the use of any data from comparative morphology, or from paleontology, or from phylogeny. These, when correct, should support or undermine his theory.

Even if generally true, so long as there are any exceptions each case must be decided on its own merits and therefore size of range or number of species can never be a complete criterion for age.

No allowance is made for extinction of old groups which must be of as common occurrence as formation of new ones. This is the main objection. A genus both at its inception and at its extinction should contain one species. This Willis disregards, with the result that mature groups are called "old," and both young and old groups are called "young."

The following cases of Salamander distribution, in which relative age of groups is determined by comparative morphology and phylogeny, will serve to illustrate Age and Area.

The family *Hynobiidæ* contains five genera. The most primitive of these, *Hynobius,* contains fifteen species and has an enormous range, throughout northern Asia. It has given rise to four more specialized genera, three of them monotypic, and one with two species. These four daughter genera have very restricted ranges, three (and probably all) within the range of the parent genus.

Here evidently the oldest genus has the widest range and the greatest number of species. But the accepted ages of the groups do not rest upon size of range or upon number of species. They rest upon the comparative morphology of the forms.

In the *Plethodontidæ* the most primitive genus is *Gyrinophilus* with two species and a moderate range. The most specialized is *Leurognathus* with one species and a very restricted range. The largest genus *Œdipus* is much less primitive than *Gyrinophilus* and hence younger, but as it has given rise to one daughter genus it is neither the oldest nor the youngest, and should properly be considered mature and successful.

Willis has presented a theory which is sometimes, as in the case of the *Hynobiidæ,* supported by the facts; and sometimes, as in the case of the *Plethodontidæ,* both supported and contradicted. Age can only be determined by careful phylogenetic work, and attempts to determine it by computation are excellent examples of the use of statistics in support of conclusions to which they are irrelevant.

Thus the facts of distribution in one small group afford support to both sides of two much contested arguments. To paraphrase Wilde, "The only general rule is that there is no general rule."

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FAMILY RESEMBLANCES AMONG AMERICAN MEN OF SCIENCE

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III. THE INFLUENCE OF THE NEARNESS OF KINSHIP

IT would seem reasonable to suppose that the nearer men are in "blood relationship," the greater would be the resemblance in performance. Brothers are more nearly related than father and son; do the brothers of distinguished men of science outnumber the sons, or the fathers, or the uncles? It has been shown that brothers resemble each other in performance in science more than cousins. In proportion to their numbers about five times as many brothers of starred men obtain positions in the starred group as cousins. Is there an increasing number of distinguished relatives with increasing closeness of relationship? The results recorded in this chapter show that there is.

DEGREES OF KINSHIP

If for no other reason than that reproduction of human beings is bisexual it is reasonable to suppose that brothers are more nearly related than cousins or than grandsons and grandparents. The zygotes from which brothers grow are each the result of a combination of individual cells (gametes) from two different groups of cells. If we assume that the germ cells from the male vary about a common point which in turn varies from the common point of the species, the chances are that the offspring will vary from the mid-measure of the species in the direction of the variation of the parent. If we assume that the parent's qualities give a clue to the kind of germ cells he carries, that is, if we assume that a man of genius carries germ cells which vary as a group from the germ cells of the species and that the average of these variable

cells of the individual closely resembles the zygote from which the man developed, the chances are certainly remote that the maternal side will furnish a gamete for the union that will maintain the zygotic resemblance.

The problem of apparent blending in resemblance as in the case of pigmentation of offspring of negroes and whites and of Mendelian or alternative inheritance in the case of eye color are beyond the scope of this study. Biologists do not seem to be agreed on the decree to which one may generalize, as the following quotation would seem to show:

> It seems best, accordingly, to attempt neither with Galton to generalize all inheritance as blending nor with Johannsen to treat all inheritance as alternative, but frankly to recognize the existence of two categories of cases distinct in their inheritance behavior.[1]

Whatever the method, blending or alternative or both without a very exact assortive mating the union of two gametes will produce an individual that is as a matter of chance less likely to resemble either parent than if the individual developed asexually. This factor, then, would tend to decrease the resemblance of near relatives to a degree that would vary as the number of matings is involved. If the gametes of any individual actually vary about an average that is approximated by the zygote from which the individual who carries them grew, it is likely that of two brothers one carries a group of germ cells superior, on the average, to the germ cells of the other. It is conceivable that the "inferior" of the two carries a group of cells superior to the "superior" brother. Speculations of this sort belong to workers more familiar with experimental genetics. They are given as suggestions of the complications of the apparently simple problem of determining the relative influence of the different ancestors.

DISTINGUISHED RELATIVES IN EACH DEGREE OF KINSHIP

Whatever the values of the intervals between the different relationships may be, the following order is

[1] W. E. Castle, "Genetics and Eugenics," 1916, p. 218.

assumed to be valid in the sense that closeness varies according to the following order:

(1) Brother and sister
(2) Father, mother, son and daughter
(3) Uncle, aunt, niece and nephew
(4) Grandparent
(5) Cousin

The details concerning the number of relatives of distinction in each specific relationship are given in table four but they are repeated as part of table six to facilitate comparison. It will be noted that the specific kinships recorded in this table are arranged in the assumed order of nearness.

TABLE VI

	Detailed Grouping		Totals of Each in Course Grouping
Brothers and sisters	B	146	
	Si	13	159
Sons, daughters, fathers and mothers	S	18	
	D	1	
	F	78	
	M	3	100
Uncles, aunts, nieces and nephews	FB	33	
	FSi	4	
	MB	31	
	MSi		
	BS	6	
	BD	3	
	SiS	3	
	SiD		80
Grandparents	FF	17	
	FM	1	
	MF	35	
	MM	1	54
First cousins	FBS	45	
	FBD		
	FSiS	15	
	FSiD	2	
	MBS	20	
	MBD	1	
	MSIS	18	
	MSiD	4	105
Total	Total	498	498

It is obvious that the raw totals in the course grouping are without significance except as they give a sort of bird's-eye view of the situation. It can be seen at a glance that eight specific first cousin relationships do not furnish as many relatives of distinction as the two relationships of brother and sister. The comparison is no less striking if only the males are considered. In this comparison there are 146 brothers and 98 first cousins. These two groups happen to be rather directly comparable, the factors making for inclusion of those of the one group about equalling the factors making for inclusion of members of the other. But the other relationships and the source of those included make certain considerations of importance necessary. Two of these considerations are (1) the number of persons in each specific relationship, that is, the number of brothers, the number of sisters, the number of mothers, fathers, the number of individuals in each one of the eight first cousin kinships and so on; (2) the equality of certain of the chance factors determining inclusion for the different groups in any one of the handbooks by which distinction is measured.

In direct ancestry the number in each degree of kinship is obvious. A man has in each and every specific ancestral relationship one relative. He has one father, one mother, one FF, one MF, one FFF, and so on *ad infinitum*. Furthermore, each of the individuals in the direct ancestry reaches an adult age, if ability to reproduce is a measure of maturity. Certainly, all do not reach the average age at which men obtain a place in a biographical handbook. Age and number of offspring have a positive correlation, however.

In the collateral ancestry and in descendants the number does not lend itself so easily to deduction. In a stationary population the average number of fertile relatives in each specific kinship would equal the number of ancestors in each specific relationship, which has been shown to be one.[2] Furthermore, Galton, in the work just

[2] Noteworthy families, Galton and Schuster, p. 33.

cited, proposes: "that the number of fertile individuals is not grossly different to that of those who live long enough to have an opportunity of distinguishing themselves."

Galton's study dealt with the families of members of the Royal Society living in 1904. The data concerning the near relatives of 100 of these men were collected and the findings on the number in each specific relationship are given in the table below (see Table VII).[3]

TABLE VII

Kinship (Males)	Number	Kinship (Females)	Number
Brothers	206	Sisters	207
Uncles (FB)	228	Aunts (Fsi)	207
Uncles (MB)	219	Aunts (MSi)	238
Cousins (FBS)	263	Aunts (FBD)	302
Cousins (FSiS)	184	Aunts (FSiD)	208
Cousins (MBS)	236	Aunts (MBD)	266
Cousins (MSiS)	237	Aunts (MSiD)	246
Totals	1575		1674
Average per man	2.25		2.39

For our purposes these data are important in showing that whatever the number of relatives in specific degrees of relationship may be, it is approximately the same for those relationships other than direct ancestry. Direct ancestry can not include infertile people; collateral ancestry and direct descendants furnish the infertile part of the population, that is, those who die before maturity and those who reach maturity but do not reproduce. If the above is a correct analysis, it would seem proper to compare the direct ancestors, coming from a stationary population, with each other, allowing only for the relative number in each degree. Such an arrangement would result in an order beginning with the father-mother relationship of two and would increase by doubling in each successive degree of remoteness, as follows:

Father–mother 2
Grandparent 4
Great-grandparents, etc. 8

[3] *Ibid.*, p. 30.

The progression for the collaterals and descendants, beginning with the brothers, would be:

Brother–sister	$2 + 2x$[4]
Son–daughter	$2 + 2x$
Uncle–aunt	$4 + 2x$
First cousin	$8 + 8x$

Owing to the completeness of the reports by the men of science it is possible to determine, that for the brothers and sisters X is not smaller than .22. For 1,000 men of science the computations showed 1,264 brothers and 1,180 sisters, *i.e.*, 2,440 siblings, living at the time the replies to the questionnaire were sent in. This means that there were 2.44 siblings per man in these relationships, or approximately 1.26 per brother relationship and 1.18 per sister relationship. It seems reasonable to suppose that these figures are too high. The death rate among the professional classes is said to be lower than among the generality, but such a low death rate as these figures would indicate is probably incorrect. If a comparison were to be made between the direct ancestors and the collaterals in which the unit value in the former be called one and the unit value in the latter be called 1.22, it would seem that the validity would be greater than if the unit value were considered 1 in all cases as Galton proposes.

NUMBER OF DISTINGUISHED RELATIVES IN EACH DEGREE OF KINSHIP

It now becomes necessary to examine more carefully the method of determining distinction, since three handbooks, covering somewhat different periods, and with different selective standards, were used.

Both editions of "American Men of Science," that is, the editions of 1903 and 1910, were consulted, and biographies found in either were counted. Those found in the original edition of Appleton's "Cyclopedia," published in 1887–8, together with the appendix of 1890 and

[4] X equalling the number that must be added to one to make up for those who die before reaching maturity or who do not reproduce though they reach maturity.

all ten volumes of "Who's Who in America" covering the period from 1910 to 1918 were also included. The first edition of "American Men of Science" contains more than 4,000 men of science, of entire North America, the second edition of 1887–88 of Appleon's Cyclopedia of American Biography contains "above 15,000 prominent native and adopted citizens of the United States, including living persons, from the earliest settlement of the country." In the appendix of 1890–00 "will be found nearly 2,000 notices of Americans who won renown in the war with Spain . . . and of persons of the New World who have become prominent in the peaceful activities of life during the decade" between the appearance of the two publications. The ten volumes of "Who's Who in America" contain 36,915 biographical sketches. The first volume contains 8,602 biographies, while volume 10 has 22,968. It is evident that the three publications have varying standards of selection, and it becomes necessary to get some statement of the degree of fineness of selection represented by each.

Appleton's "Cyclopedia" covers a period of nearly four hundred years. The small population in the early periods with which it is concerned, and the probability that the later periods, namely, the periods during which the grandparents and older fathers of the men of science might have been included, are unduly favored has led the writer to assume a fineness of selection of double that of "Who's Who in America," or one in 2,500 of the generality. Whether this guess has any great validity does not greatly affect the major part of the results in this chapter. If the reader has reason to doubt the proportion, the comparisons of the grandparents with the other relatives may be ignored. The grandparents are the only important group affected.

The ten volumes of "Who's Who in America" that were used are reported by the editors (see preface of Vol. 10, 1918–19) to contain 36,915 individual biographies for a period covering nearly 20 years. The varying numbers

in the different volumes do not correspond in relative size with the changes in population. The population of the United States in 1900 was 75,000,000, in 1910 it was 92,0000,000, in 1920, if the growth followed the curve of growth during the two preceding decades, 110,000,000. The ratio of 8,602 to 75,000,000 is approximately 1 to 8,700. The ratio of 22,968 to 92,000,000 is 1 to 5,243 for the generality. For 1912–13, it is 18,794 to 94,000,000 estimated or 1 to 5,000 of the total population. Since the majority of the biographies of relatives found in "Who's Who in America" are in the later editions, and since the editors omit mention in each succeeding edition of a considerable number of those in a previous edition, the ratio of 1 to 5,000 will be used.

Of the 498 relatives of distinction there are 33 whose biographies are found in "American Men of Science" exclusively, and, owing to the specialized requirements for inclusion, this book is used only for special cases described below. No special consideration is given, therefore, to the fineness of selection, other than that used in part II.

Table VIII gives what seems to be the most important facts concerning the distribution of relatives of distinction in the various relationships. Some of the reasons for limiting the comparisons to the specific relationships have been given and certain justifications for including the fathers, who are direct ancestors, with the others who are collateral relatives have been implied. The full number of fathers who reached the required average age is probably less than the number of brothers found to have reached this age. However, practically all fathers had had full opportunity to become distinguished, whereas not all brothers and first cousins had. On the other hand, the fathers who died before the first issue of "Who's Who in America" had less opportunity to be included in other than Appleton's "Cyclopedia." The uncles present somewhat the same problem as the fathers, except for number.

The sons, daughters, nieces and nephews are excluded from this comparison by age. Diminishing birthrate also makes such direct comparison of the younger members with the older impossible.

TABLE VIII

DISTRIBUTION OF DISTINGUISHED RELATIVES ACCORDING TO DEGREE OF KINSHIP

Relationship	Distinguished Relatives (1)	Number of Relatives Reduced to Comparable Ratios (2)	Facts of Column Two Expressed in Per Cent. (3)
Brothers and sisters	140	140	50.5
Fathers and mothers	78	78	28.2
Uncles and aunts	68	34	12.3
First cousins	100	25	9.0
Total	386	277	100.0
Distribution of Males			
Brothers	127	127	49.4
Fathers	75	75	29.1
Uncles	64	32	12.5
Cousins	93	23	9.0
Total	159	257	100.0
Distribution of Females			
Sisters	13	13	65.8
Mothers	3	3	15.2
Aunts	4	2	10.1
Cousins	7	1.75	9.0
Total	27	19.75	100.0
Distribution of Males with Grandfathers Included			
Brothers	127	127	44.9
Fathers	75	75	26.5
Uncles	64	32	11.3
Grandfathers	52	26	9.2
Cousins (male)	93	23	8.1
Total	411	283	100.00

Since all of the 52 distinguished grandfathers were recorded in Appleton's "Cyclopedia" and since it was

assumed that the fineness of selection of that handbook was greater than the other handbooks, it seems probable that the per cent. column is invalid in that relationship. There remain the more valid differences in the brother and cousin relationship and in the father-uncle groups.

According to the figures in Table VIII, a person from the brother-sister relationship is almost twice as likely to be distinguished as one from the father-mother relationship, four times as likely as one from the uncle-aunt group and between five and six times as likely as one from the cousin group. The females are too few in number to make such comparisons valid for them. They are given in the separate section of Table VIII because the reader may be interested in their distribution in spite of the small number. Probably the most valid difference is that found in the comparison of the number of brothers and cousins who obtained a position in the starred group. From four times as many male cousins as brothers came fewer starred men.

I have computed similar ratios from the proportions reported by Galton [5] in his study of relatives of living fellows of the Royal Society whose names appeared in the year book of the society in 1904. Only male relatives are represented, and are as follows:

TABLE IX

	Number	Number of Relatives Reduced to Comparable Ratios	Expressed in Per Cent.
Brothers	104	104	40.3
Fathers	81	81	31.4
Uncles	97	48.5	18.8
Cousins	99	24.75	9.5
Total	381	258.25	100.0

In any judgment of the validity of the differences given above it is well to keep in mind the fact that the near relatives are more likely to be recorded and reported than

[5] Noteworthy Families, p. xl.

the more remote. One might say that completeness of data is correlated directly with closeness of relationship, owing to the less exact knowledge concerning the more remotely related. Omissions are more likely to occur in the cousin relationships than in the brothers and more likely in the uncle relationship than in the fathers.

Something of a check on results already given may be had by comparing the distribution of nephews and nieces with sons and daughters. Both groups should be comparable so far as age and numbers are concerned. Furthermore, all handbooks may be used since all persons concerned have had equal opportunity to achieve a place in the various lists. None is included in Appleton's "Cyclopedia."

TABLE X

Relationship	Number of Those Distinguished	Reduced to Comparable Ratios	Reduced to Per Cent.
Sons and daughters.....	18	18	75
Nieces and nephews.....	12	6	25
Total.....	30	24	100

The small number in each of the two groups does not permit any great confidence in reliability of the ratios, but the results are in agreement with the previous table. Table IV shows that five of the sons are found only in "American Men of Science." It might, therefore, be argued that a contributing factor causing the larger number of sons to be distinguished is the direction of the work. Sons, at least English sons, are said to be more likely than not to follow the occupation of the father. Since "American Men of Science" is restricted to scientific people and is a less fine selection than "Who's Who in America," the sons of scientific men are more likely to be included than sons and daughters of the uncles and aunts. If we eliminate those found only in "American Men of Science," we have the following:

TABLE XI

	Number Distinguished	Reduced to Comparable Ratios	Reduced to Per Cent.
Sons and daughters.....	13	13	70.3
Nieces and nephews.....	11	5.5	29.7
Total.....	25	18.5	100.0

It will be seen that the per cent. ratios remain substantially the same.

It is likely that the sons and daughters who are distinguished are more completely recorded than the nieces and nephews. The fact remains that these data are in agreement with those of all like studies. The nearer the kinship the greater the resemblance in distinction, and if distinction means special performance, the greater the resemblance in performance.

RELATIONSHIPS MORE REMOTE THAN FIRST COUSIN

Numerous relatives of more remote degree than first cousin were reported and others were discovered by the writer. There were 60 first cousins of the parents of the men of science. Of these, 31 are cousins of the father and 29 cousins of the mother. The numbers are consistent with the other data, but the possibilities of error and incompleteness make the account of these and other remote relatives unusable at present except in the study of specialization of inheritance. The tedious and exacting work of deciphering relationships in remote degrees make the usefulness of doing so questionable in the present case.

There are 53 great uncles and great aunts, that is, uncles and aunts of the parents of the scientific men. This, again, is in agreement with the rest of the data. There are 21 great-grandparents. There are 82 relatives of a degree more remote than any mentioned and 43 of remote relationship, but of a degree not yet determined. A simple summary of these extra-statistical relatives is as follows:

TABLE XII

First cousins of parents:	
(1) Cousins of father	31
(2) Cousins of mother	29
Great-uncles and aunts:	
(1) Uncles of father	28
(2) Uncles of mother	25
Great-grandparents:	
(1) Grandparents of father	8
(2) Grandparents of mother	13
More remote than any listed above	82
Total	217
Relationship unknown but known to be at least as remote as cousin of parent	43
Total	260

The Number of Paternal and Maternal Relatives of Distinction

Table XIII gives the distribution of relatives of distinction in two groups, the paternal and the maternal. The equality of the two groups is obvious. The differences in specific relationships, such as grandparents and cousins, may be of significance, but none is known. The difference in favor of the MF is, in fact, striking, but if explained as indicative of some advantageous maternal inheritance, some explanation for the size of the FBS group must be found.

TABLE XIII

Relatives on Paternal Side Fathers Omitted		Relatives on Maternal Side Mothers Omitted	
FB	33	MB	31
FSi	4	MSi	
FF	17	MF	35
FM	1	MM	1
FBS	45	MBS	20
FBD		MBD	1
FSiS	15	MSiS	18
FSiD	2	MsiD	4
Total	117	Total	110

More Remote Relatives

Cousins of father	31	Cousins of mother	29
Uncles of father	28	Uncles of mother	25
Grandparents of father	8	Grandparents of mother	13
Total	67	Total	67

The perfect agreement in the totals of the more remote relatives is indicative of a high degree of validity in the data, as are the totals in the near relatives account. The evidence for the truth of this statement is found in Galton's studies. His early studies, in which remote relationships were used, showed paternal relatives predominating over maternal at a ratio of seven to three. This ratio held closely for five of the eight groups of distinguished men. In two of the other three the differences were greater, being 95 to 6 for 16 relatives of great poets and 85 to 15 for 20 relatives of artists. The divines, however, showed an opposite ratio of 27 to 73.

Galton seemed to take these differences rather seriously and offered some curious explanations, such as possible lack of feminine attraction in women of families of high intellectual merit. But in his later work on "English Men of Science," he says:

> As regards the relative influence of paternal and maternal lines I find close equality. My method of comparison is by setting off paternal grandfathers and maternal uncles, no other degree of kinship being available for the purpose. My results for 100 scientific men are paternal grandfathers, public characters, 10, of high private reputation 3, paternal uncles 13 and 8, making a total on the paternal side of 34. On the other hand, the maternal grandfathers are 11 and 4, maternal uncles, 15 and 7, making a total on the maternal side of 37. . . . In Hereditary Genius, p. 196 having fewer cases to deal with I extended my inquiries to nephews and grandsons, and in a second table to great-grandparents, grandsons and other equally remote degrees, but this latter was confessedly of little value.[6]

The similarity in paternal and maternal groups holds in the case of science. There is a difference in favor of the maternal group, but it is thought that this difference is within limits determined by chance factors. The total number in the paternal group is 117, of whom 30.8 per cent. are classed as people of distinction in the field of science. The total number in the maternal group is 110, of whom 36.3 per cent. are classed as people of distinction in the field of science.

From a common-sense point of view these similarities are certainly unexpected. One would think that the di-

[6] English Men of Science, 1874, p. 72.

TABLE XIV

MATERNAL AND PATERNAL RELATIVES DISTINGUISHED IN SCIENCE AND IN FIELDS OTHER THAN SCIENCE

Paternal			Maternal		
	Science	Non-science		Science	Non-science
FF	3	14	MF	10	25
FM		1	MM		1
FB	7	26	MB	9	22
FSi		4	MSi		
FBS	21	24	MBS	10	10
FBD			MBD	1	
FSiS	5	10	MSiS	9	9
FSiD		2	MSiD	1	3
	36	81		40	70
Totals	117			110	
Differences in per cent	30.8	69.2		36.3	63.7

rection of a man's work is more likely to be directed by paternal social inheritance than maternal. The son has direct contact with the occupational activity of the father; his contact with the occupations of those on the maternal side are indirect in the sense that the mother is not likely to be engaged in a specific field other than domestic duties. Explanation can be made from the sociological or biological points of view; the fact remains that whatever environmental factors are causes of the direction and extent of achievement, there is no evidence of differential influence in paternal and maternal directions.

It is not unreasonable to expect that future ratings of youthful individuals for whom psychologists will predict a future will take account of the performance of their relatives. It is being proposed that more just methods of insurance would be in force if differential ratios were allowed on the basis of the length of life of the parents and grandparents of the person desiring insurance. Biologists and actuaries propose to predict length of life by "performance" of near relatives. It may be possible

to equate the values of the different degrees of relationship as an item in the prediction of achievement.

The method used in this study has serious limitations, but in the present state of ignorance and difficulty of making measurements of the performance in question it gives results that are believed to be a distinct contribution to the fund of information on family resemblances. It may be that adequate measures of high intellectual performance will soon be discovered and perfected, but an enormous amount of measuring must be done before ideally scientific methods can give the data equivalent to that contained in this study. The long period concerned in the history of one generation, the difficulty of making objective measurements on closely related, and much more on the remotely related, together with the expense and persistence required, justifies the present method in spite of the limitations. We are referring now to intellectual performance of such an order that the life history of the individual becomes of public interest.

SUMMARY

The data show (1) that a brother of a man of science is twice as likely to be distinguished as a father, four times as likely as an uncle and about six times as likely as a first cousin, and offspring three times as likely as nieces and nephews; (2) that paternal and maternal influences are not unequal; (3) that the number of relatives in the remote degrees though not strictly comparable show results consistent with the more complete accounts of those in the nearer.

(To be continued)

EXPERIMENTAL STUDIES ON THE DURATION OF LIFE

VII. The Mendelian Inheritance of Duration of Life in Crosses of Wild Type and Quintuple Stocks of Drosophila Melanogaster[1]

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Introduction

There is now abundant evidence from at least two widely different organisms, *Drosophila* and man, that if duration of life be measured accurately for a considerable number of individuals, and these measurements be then treated as attributes or characters of the individuals which gave rise to them, the results over a series of generations are in fact precisely as they would be expected to be if duration of life were an inherited character, like stature or eye color (*cf.* Pearl, R. (52), for a review of the literature on which this statement is based). In the case of man the evidence is in the main statistical in character (but see Pearl, R. (53)) and gives directly no inkling as to the mechanism of the inheritance. In *Drosophila* Hyde (11) showed that the character appeared to be inherited in a Mendelian manner, and Pearl and Parker (32) have demonstrated the constancy of definite degrees of mean longevity in inbred strains or lines of the same organism. There is needed, however, much more intensive investigation of the exact mode and mechanism of inheritance of this character in *Drosophila,* in spite of the excellent pioneer work of Hyde, which we have been able to confirm in every essential particular. This and the next following paper in this series will be devoted to the discussion of results which have so far been obtained in this field

[1] Papers from the Department of Biometry and Vital Statistics, School of Hygiene and Public Health, Johns Hopkins University. No. 84.

in the work of this laboratory. The present paper will give the analysis of data resulting from extensive experiments in crossing wild type flies of our Old Falmouth stock (*cf.* Pearl and Parker (27, p. 486)) with the short-lived Quintuple stock.

Complete life tables for wild type flies, of which the Old Falmouth stock is representative, and for Quintuple flies, have been presented in the first of these Studies. The wide difference in the two stocks crossed in the present experiments is sufficiently indicated by the fact that for wild type males the expectation of life (e_x) at emergence is 41.0 days and for Quintuple males is only 14.2 days. For females the corresponding e_x figures are 38.8 and 15.8 days, respectively. We are thus dealing with well-defined, indeed widely different, grades or degrees of the character in the two stocks in these experiments.

MATERIAL AND METHODS

The data on duration of life of the parental stocks used in these experiments were obtained from the progeny of 4 individual (brother and sister) matings in each of the two stocks Old Falmouth and Quintuple, made on April 7–9, 1920. The offspring flies emerged between April 17 and May 5, 1920. The original parents were transferred to new mating bottles 8 days after the first bottle, in each case, was started.

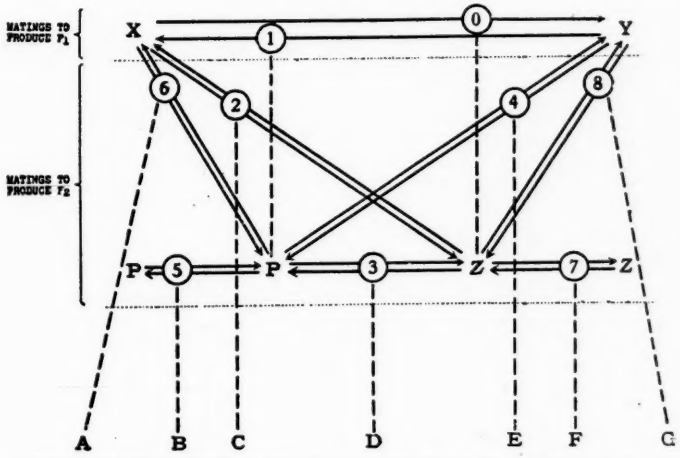
The F_1 flies were derived from one mass mating of each of the possible reciprocal crosses. These matings were of 6 pairs of flies each, taken at random from the stock bottles of the two sorts used. The matings were made April 20, 1920, and the flies emerged April 30–May 14. The parents were transferred to new breeding bottles 8 days after the first bottles were started.

The matings to produce F_2 and F_3 generations are designated throughout this paper on the standard plan described some years ago by Pearl (54). In order to save reference to that paper Table I is reproduced from

it here. In the present case X = Quintuple, and Y = Old Falmouth.

TABLE I

MATINGS TO PRODUCE F_2



F_2 Individuals Mated	Number of Mating	F_2 Individuals Mated	Number of Mating	F_2 Individuals Mated	Number of Mating	F_2 Individuals Mated	Number of Mating
$A \times X$	10	$B \times Z$	46	$C \times F$	51	$E \times E$	19
$A \times Y$	12	$B \times B$	13	$C \times G$	53	$E \times F$	45
$A \times P$	40	$B \times C$	37	$D \times X$	22	$E \times G$	47
$A \times Z$	42	$B \times D$	29	$D \times Y$	24	$F \times X$	30
$A \times A$	11	$B \times E$	55	$D \times P$	52	$F \times Y$	32
$A \times B$	33	$B \times F$	57	$D \times Z$	54	$F \times P$	60
$A \times C$	25	$B \times G$	59	$D \times D$	17	$F \times Z$	62
$A \times D$	35	$C \times X$	18	$D \times E$	43	$F \times F$	21
$A \times E$	61	$C \times Y$	20	$D \times F$	31	$F \times G$	49
$A \times F$	63	$C \times P$	48	$D \times G$	27	$G \times X$	34
$A \times G$	65	$C \times Z$	50	$E \times X$	26	$G \times Y$	36
$B \times X$	14	$C \times C$	15	$E \times Y$	28	$G \times P$	64
$B \times Y$	16	$C \times D$	39	$E \times P$	56	$G \times Z$	66
$B \times P$	44	$C \times E$	41	$E \times Z$	58	$G \times G$	23

Table II gives the data regarding the matings to produce the F_2 and F_3 generations.

In all the experiments recorded in this paper the only one of the five somatic mutant characters carried in the Quintuple stock to which any attention was paid was *vestigial wing*. Individuals were not recorded at all in

TABLE II

DATA ON MATINGS TO PRODUCE F_2 AND F_3

General Type of Mating	Type of Progeny Flies	Type of Mating	Mating No.	Date of Mating (all 1920)	Type of Parents		No. Parents Mated		Date of Emergence of Parents		Date of Emergence of Progeny	No. of Progeny	
					♂	♀	♂	♀	♂	♀		Wild Type	Vestigial
$F_1 \times F_1$	F	(7)	72	5/1	Z	Z	4	4	5/1	5/1	5/10–18	115	19
$F_1 \times F_1$	B	(5)	73	5/1	P	P	4	4	5/1	5/1	5/10–18	56	7
$F_1 \times F_1$	F	(7)	74	5/4	Z	Z	6	6	5/4	5/4	5/13–21	109	22
$F_1 \times F_1$	B	(5)	75	5/4	P	P	6	6	5/4	5/4	5/13–21	146	56
$F_1 \times F_1$	D	(3)	76	5/20	P	Z	2	2	5/8	5/8	5/29–6/6	115	10
$F_1 \times F_1$	D	(3)	77	5/20	Z	P	2	2	5/7	5/8	5/29–6/6	98	34
												639	148
$F_1 \times$ Quintuple	C	(2)	78	5/20	Quin.	Z	1	1	5/20	5/13	5/28–6/4	64	72
$F_1 \times$ Quintuple	C	(2)	79	5/20	Z	Quin.	4	4	5/7	5/20	5/30–6/6	24	44
$F_1 \times$ Quintuple	A	(6)	82	5/20	Quin.	P	1	1	5/20	5/8	5/29–6/6	75	70
$F_1 \times$ Quintuple	A	(6)	83	5/20	P	Quin.	4	4	5/8	5/20	5/29–6/6	54	80
												217	266
$F_1 \times$ Old Fal.	G	(8)	80	5/20	O.F.	Z	1	1	5/20	5/13	5/28–6/5	142	—
$F_1 \times$ Old Fal.	G	(8)	81	5/20	Z	O.F.	4	4	5/7	5/20	5/30–6/6	175	—
$F_1 \times$ Old Fal.	E	(4)	84	5/20	O.F.	P	1	1	5/20	5/8	5/28–6/5	163	—
$F_1 \times$ Old Fal.	E	(4)	85	5/20	P	O.F.	4	6	5/8	5/20	5/29–6/6	202	—
												682	—
F_1 ♂ $\times$ F_2 Vest. ♀	—	54	86	6/1	Z	D_{76}	3	3	5/9	5/29	6/9–17	76	121
F_1 ♂ $\times$ F_2 Vest. ♀	—	52	88	6/1	P	D_{76}	3	3	5/10	5/30	6/10–18	95	107
F_1 ♂ $\times$ F_2 Vest. ♀	—	54	90	6/1	Z	D_{77}	3	3	5/9	5/29	6/9 –17	67	76
F_1 ♂ $\times$ F_2 Vest. ♀	—	52	92	6/1	P	D_{77}	3	3	5/10	5/29	6/9 –17	63	119
												301	423
F_1 ♂ $\times$ F_2 Wild ♀	—	54	87	6/1	Z	D_{76}	3	3	5/9	6/1	6/10–18	155	55
F_1 ♂ $\times$ F_2 Wild ♀	—	52	89	6/1	P	D_{76}	3	3	5/9	5/30	6/9 –17	175	0
F_1 ♂ $\times$ F_2 Wild ♀	—	54	91	6/1	Z	D_{77}	3	3	5/9	5/28	6/10–18	163	2
F_1 ♂ $\times$ F_2 Wild ♀	—	52	93	6/1	P	D_{77}	3	3	5/9	5/28	6/9 –17	152	7
												645	64

respect of the other four, purple, speck, arc and black. This was deliberate. We desired to deal only with that one of the five mutations which earlier experiments had shown to be definitely and markedly related to duration of life, and which at the same time easily identified the flies morphologically. In the next paper in this series each of the 5 mutations in Quintuple will be dealt with separately in relation to duration of life. The experiments here recorded were all carried out in accordance with the standard procedure described in the earlier papers in this series. All determinations of duration of life were made in incubators at 25° C. The food and other environmental conditions were as constant and identical for all groups as it was possible to make them. In tabulating and analyzing the results both sexes are treated together.

TABLE III

DEATH AND SURVIVORSHIP DISTRIBUTIONS FOR P AND F_1 GENERATIONS

Age in Days	Old Falmouth		Old Falmouth ♂ × Quintuple ♀ (Mating Type (1))		Quintuple ♂ × Old Falmouth ♀ (Mating Type (0))		All F_1's		Age in Days	Quintuple	
	d_x'	l_x'	d_x'	l_x'	d_x'	l_x'	d_x'	l_x'		d_x'	l_x'
1– 5	19	1,000	1	1,000	2	1,000	3	1,000	1– 2	19	1,000
6–11	14	970	0	993	6	994	6	993	3– 5	27	953
12–17	21	948	2	993	5	977	7	982	6– 8	47	886
18–23	27	915	7	980	4	962	11	968	9–11	71	769
24–29	38	872	12	934	22	951	34	946	12–14	72	592
30–35	63	812	6	854	16	887	22	877	15–17	66	413
36–41	65	712	12	815	16	841	28	833	18–20	43	249
42–47	90	609	9	735	61	795	70	777	21–23	18	142
48–53	84	467	18	675	43	618	61	636	24–26	19	97
54–59	107	334	37	556	61	494	98	513	27–29	10	50
60–65	72	165	27	311	42	318	69	316	30–32	6	25
66–71	23	51	14	132	41	197	55	177	33–35	3	10
72–77	7	14	6	40	24	78	30	66	36–38	1	2
78–83	0	3	—	0	3	9	3	6	39–41	—	0
84–89	2	3	—	—	—	0	—	0	--	—	—
90–95	—	0	—	—	—	—	—	—	—	—	—
Totals	632	—	151	—	346	—	497	—	—	402	—

PARENTAL AND F_1 GENERATIONS

The observed death distributions and the survivorship distributions calculated therefrom, for (a) the two parental stocks, (b) the F_1 individuals from reciprocal crosses, and (c) the combined F_1's are given in Table III. In this and all similar tables throughout the paper, the figures entered in the d_x' columns are the observed number of flies dying *within* the age interval indicated in the age column, and the figures in the l_x' column are the numbers of survivors out of 1,000 starting imaginal life together, *at the beginning of each age interval.*

The survivorship distributions of Table III are shown graphically, on an arithlog grid, in Fig. 1.

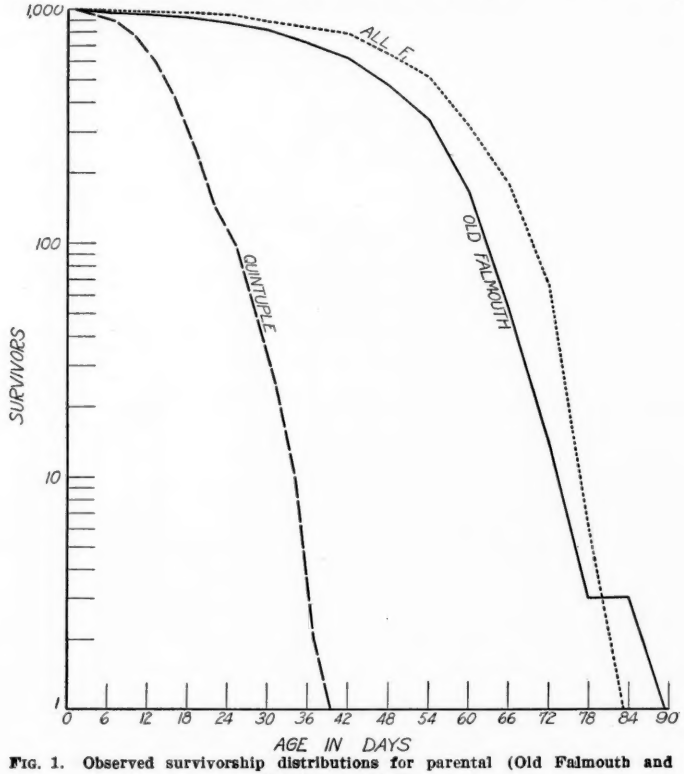


FIG. 1. Observed survivorship distributions for parental (Old Falmouth and Quintuple) and F_1.

The biometric constants calculated from the d_x' distributions of Table III are presented in Table IV.

TABLE IV

BIOMETRIC CONSTANTS FOR DURATION OF LIFE OF PARENTAL AND F_1 FLIES

	Group	Mating Type	Mean Age at Death	Standard Deviation	Coefficient of Variation
Parental	Old Falmouth.....	—	44.26±.44 days	16.57±.31	37.44± .80
	Quintuple.....	—	14.08±.23 days	6.93±.16	49.23±1.43
F_1	Quint. ♂ × Old Fal. ♀	(0)	51.73±.57 days	15.71±.40	30.37± .85
	Old Fal. ♂ × Quint. ♀	(1)	51.12±.84 days	15.29±.59	29.90±1.26
	All F_1's	(0)+(1)	51.55±.47 days	15.58±.33	30.23± .70

From the data so far presented we note the following points:

1. In these experiments we are crossing two strains of *Drosophila* of widely different average duration of life and forms of life curve. The wild type Old Falmouth parent stock has a mean duration of life more than three times as great as that of the Quintuple parent stock. This difference is so great, and the two stocks are so constant in the maintenance of their characteristic mean longevities, that there can be no question that we are crossing two distinct biological entities perfectly discontinuous in respect of the character dealt with. The two stocks differ fundamentally not only in respect of mean duration of life but also in respect of variation in the time of dying.

2. The F_1 generation progeny from the cross are structurally like the wild type parent. That is to say, the F_1 flies are to a first degree of approximation indistinguishable in their morphology from the wild type parent. The morphological mutations carried by the Quintuple flies behave as Mendelian recessives to their wild type allelomorphs. Also the duration of life in the F_1 flies is essentially similar to that established by their wild type (Old Falmouth) parent. They are long-lived flies. In actual fact the F_1's have a somewhat longer mean duration of life than the long-lived, wild type par-

ent. Taking all F_1's together the difference in the mean is $51.55 - 44.26 = 7.29 \pm .64$ days. This is a certainly significant difference amounting to 11.4 times its probable error. The l_x' lines in Fig. 1 show plainly the superior longevity of the F_1's over the longer lived parent. This phenomenon is objectively similar to the enhanced vigor observed in the first generation plants in crosses of maize, as described by East and Jones (55), Shull (56) and others. It probably has the same explanation.

3. There is no significant difference in respect of duration of life between the reciprocal crosses. The mean duration of life and the variability is identical whether the cross-bred individuals had a wild type father or mother. This is to be expected for the structural characters of the fly, at least, because none of the mutations in the Quintuple stock exhibits sex-linked inheritance, and they have therefore had their genes assigned to another (the second) than the X chromosome. Duration of life in this respect behaves in inheritance exactly like the morphological mutations with which it is associated in this cross.

4. The F_1 flies are significantly less variable relatively in duration of life than are either of the parent stocks. In view of the close parallelism between inheritance of morphological characters and inheritance of duration of life which has so far been noted (and which will be shown as we proceed to extend to many other genetic relationships), what one would like to know is whether the F_1's are less variable in structural characteristics than are the parent forms. We have no data on this point for the flies with which we have worked.

F_2 Generations

Since use was made of wing form (normal wild type versus vestigial wing) to distinguish the flies morphologically in this generation, attention is directed first to the Mendelian segregation of this structural character. Table V gives the data. In this table each mating is

TABLE V

MENDELIAN SEGREGATION IN F_2 OF NORMAL AND VESTIGIAL WING, TABULATED BY SEPARATE MATINGS

Mating Type	Numbers of F_2 Flies with Wings			Probable Errors	Deviation / P. E. Dev.	Probable Times of Occurrence of Such a Deviation in 100 Trials	Mating No.
	Normal	Vestigial	Total				
(5) P × P	56	7	63				73
Expected	*47.25*	*15.75*	*63*	±2.32	3.8	1.04	
(5) P × P	146	56	202				75
Expected	*151.5*	*50.5*	*202*	±4.15	1.3	38.06	
(5) Total	202	63	265				73+75
Expected	*198.75*	*66.25*	*265*	±4.76	.7	50	
(3) P ♂ × Z ♀	115	10	125				76
Expected	*93.75*	*31.25*	*125*	±3.27	6.5	.005	
(3) Z ♂ × P ♀	98	34	132				77
Expected	*99*	*33*	*132*	±3.36	.3	50	
(3) Total	213	44	257				76+77
Expected	*192.75*	*64.25*	*257*	±4.68	4.3	.37	
(7) Z × Z	115	19	134				72
Expected	*100.5*	*33.5*	*134*	±3.38	4.3	.37	
(7) Z × Z	109	22	131				74
Expected	*98.25*	*32.75*	*131*	±3.34	3.2	3.09	
(7) Total	224	41	265				72+74
Expected	*198.75*	*66.25*	*265*	±4.75	5.3	.05	
All *inter se*							
F_1 matings (3, 5 and 7)	639	148	787				73+75+76
Expected	*590.25*	*196.75*	*787*	±9.46	5.0	.074	+77+72+74
(2) Vest. ♂ × Z ♀	64	72	136				78
Expected	*68*	*68*	*136*	±3.93	1.0	50	
(2) Z ♂ × Vest. ♀	24	44	68				79
Expected	*34*	*34*	*68*	±2.78	3.6	1.52	
(2) Total	88	116	204				78+79
Expected	*102*	*102*	*204*	±4.82	2.9	5.05	
(6) Vest. ♂ × P ♀	75	70	145				82
Expected	*72.5*	*72.5*	*145*	±4.06	.6	50	

TABLE V (*Continued*)

Mating Type	Numbers of F_2 Flies with Wings			Probable Errors	Deviation / P. E. Dev.	Probable Times of Occurrence of Such a Deviation in 100 Trials	Mating No.
	Normal	Vestigial	Total				
(6) P ♂ × Vest. ♀	54	80	134				83
Expected	*67*	*67*	*134*	±3.38	3.8	1.04	
(6) Total	129	150	279				82+83
Expected	*139.5*	*139.5*	*279*	±5.63	1.9	20.00	
(2) All back and crosses of							
and							
(6) F_1 on Vestig.	217	252	469				78+79+82+83
Expected	*234.5*	*234.5*	*469*	±7.30	2.4	10.55	
(8) Wild ♂ × Z ♀	142	0	142				80
Expected	*142*	*0*	*142*	—	—	—	
(8) Z ♂ × wild ♀	175	0	175				81
Expected	*175*	*0*	*175*	—	—	—	
(2) Wild ♂ × P ♀	163	0	163				84
Expected	*163*	*0*	*163*	—	—	—	
(2) P ♂ × wild ♀	202	0	202				85
Expected	*202*	*0*	*202*	—	—	—	

given separately. The probable errors of the Mendelian ratios are on the basis of $\sqrt{npq}$ as the standard deviation of the class. The actual values of the probable errors are taken from the extremely useful set of "Tables of Probable Errors of Mendelian Ratios" issued by the Department of Plant Breeding of Cornell University.

In general the observed results in respect of the inheritance of vestigial wings appear at first glance to be not in especially bad accord with Mendelian expectation. There are, however, certain systematic divergences which should be noted. These are:

1. The F_1 *inter se* matings ($P \times P$, $P \times Z$ and $Z \times Z$), when taken as a whole, give a highly improbable, indeed certainly significant, divergence from the expected 3 : 1 ratio. Only 7 times in 10,000 trials with samples of 787 individuals should we expect in random sampling to get so great a deviation of fact from theory as that actually shown. The divergence is in the direction of *too few* vestigials. This divergence is due more to $P \times Z$ than to either of the other two mating types, $P \times P$ giving indeed a significantly non-divergent result.

2. The F_1 back crosses upon vestigial give a more probable, but still by no means satisfactory, agreement with theory. Only about once in 10 trials would as great (or greater) deviation as that realized be expected in random sampling. But the divergence is in the direction of *too many* vestigials.

3. The relations stated in 1 and 2 above mean that whenever the genes for vestigial were contributed to F_2 zygotes from individuals duplex for this character (but in the back crosses) the progeny showed an excess of vestigial as compared with wild type flies, whereas when the vestigial genes came from individuals simplex in respect of this character (as in the F_1 *inter se* matings) there was a defect of vestigial flies in the progeny. What may be the ultimate meaning or explanation of this fact we shall not discuss now, but it seems advisable to point it out as a fact.

TABLE VI

DEATH AND SURVIVORSHIP DISTRIBUTION FOR WILD TYPE F_2 FLIES, DERIVED FROM *inter se* MATINGS OF F_1

Age in Days	P × P (5)	P × P (5)	P × P (5)		P ♂ × Z ♀ (3)	Z ♂ × P ♀ (3)	P × Z (3)		Z × Z (7)	Z × Z (7)	Z × Z (7)		All F_1 *Inter Se* Matings 72–77	
	Mating 73	Mating 75	Total		Mating 76	Mating 77	Total		Mating 72	Mating 74	Total			
	d_x'	d_x'	d_x'	l_x'	d_x'	d_x'	d_x'	l_x'	d_x'	d_x'	d_x'	l_x'	d_x'	l_x'
1– 5	—	1	1	1,000	1	2	3	1,000	5	5	10	1,000	14	1,000
6–11	—	7	7	995	—	2	2	986	—	1	1	955	10	978
12–17	—	6	6	960	3	4	7	977	1	2	3	951	16	962
18–23	1	6	7	931	8	21	29	944	3	4	7	937	43	937
24–29	1	13	14	896	24	7	31	808	3	15	18	906	63	870
30–35	5	3	8	827	17	13	30	662	3	5	8	826	46	772
36–41	2	13	15	787	13	13	26	521	3	12	15	790	56	700
42–47	17	18	35	713	16	13	29	399	38	23	61	723	125	612
48–53	15	24	39	540	8	10	18	263	17	17	34	451	91	416
54–59	9	29	38	347	22	9	31	178	11	10	21	299	90	274
60–65	3	20	23	158	3	3	6	33	13	9	22	205	51	133
66–71	—	4	4	45	0	1	1	5	15	6	21	107	26	53
72–77	3	2	5	25	—	0	0	0	3	0	3	13	8	13
78–83	0	0	0	0	—	—	—	—	0	—	0	0	0	0
Totals	56	146	202	—	115	98	213	—	115	109	224	—	639	—

Turning now to the consideration of duration of life in the F_2 progeny we have in Tables VI and VII the data for wild type F_2 flies derived from *inter se* matings ($P \times P$, $P \times Z$, $Z \times Z$) of F_1.

The l_x' lines for the three total groups $P \times P$, $P \times Z$, and $Z \times Z$ and the original wild type parent are shown graphically in Fig. 2.

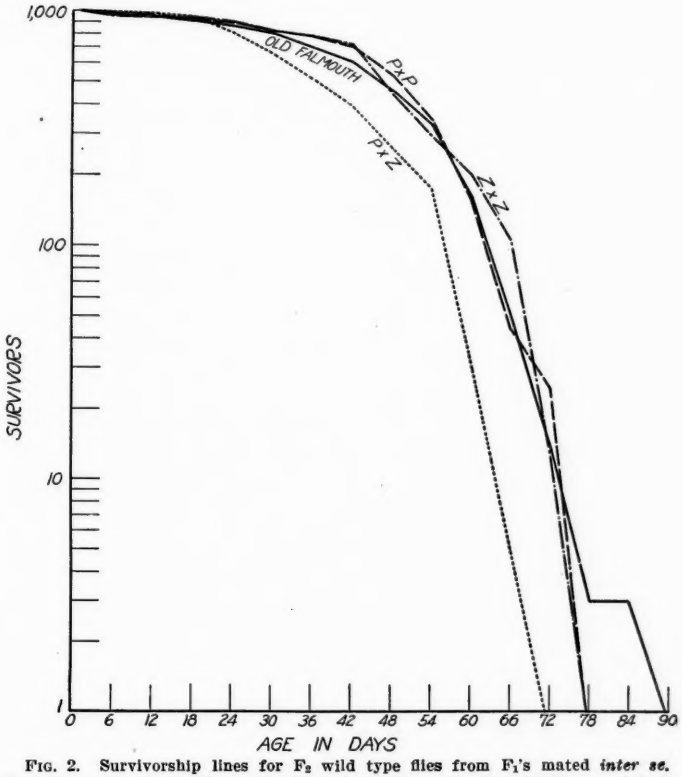


FIG. 2. Survivorship lines for F_2 wild type flies from F_1's mated *inter se*. Dash line = $P \times P$; dot line = $P \times Z$; dash-dot line = $Z \times Z$; solid line = original wild type parent stock.

From these data we note the following points regarding the wild type F_2's from *inter se* matings of F_1:

1. Taking all such flies together, they have come back almost exactly in duration of life to the same mean and

variability, both absolute and relative, as the original Old Falmouth parental stock. The segregation in respect of long life in this cross appears therefore to be quantitatively perfect, and to have followed exactly the morphological segregation of wing form, the difference of the constants for the total distribution (last line of Table VII) being not significantly different (or indeed approaching significance) from those of the Old Falmouth parent (first line of Table IV).

TABLE VII

BIOMETRIC CONSTANTS FOR DURATION OF LIFE OF WILD TYPE F_2 FLIES FROM *inter se* MATINGS OF F_1

Mating	Type	Mean Age at Death	Standard Deviation	Coefficient of Variation
P × P (Total)	(5)	46.34± .73 days	15.29±.51 days	33.00±1.22
P ♂ × Z ♀ (76)...	(3)	39.16± .83 days	13.26±.59 days	33.86±1.67
Z ♂ × P ♀ (77)...	(3)	35.89±1.01 days	14.78±.71 days	41.18±2.30
P × Z (Total)	(3)	37.66± .65 days	14.08±.46 days	37.37±1.38
Z × Z (Total)	(7)	46.01± .73 days	16.19±.52 days	35.19±1.25
All *inter se* matings.	(5)+(3)+(7)	43.33± .42 days	15.75±.30 days	36.34± .77

2. The two similar *inter se* mating types, P × P and Z × Z, give substantially identical results for duration of life, neither means nor variability differing significantly.

3. The cross *inter se* mating type, P × Z, has a significantly lower mean duration of life than either of the other two types. The differences are:

$$\text{For P} \times \text{P}, \quad 46.34 - 37.66 = 8.68 \pm .98 \text{ days}$$
$$\text{For Z} \times \text{Z}, \quad 46.01 - 37.66 = 8.35 \pm .98 \text{ days}$$

In variability there is no certainly significant difference.

The corresponding data to Tables VI and VII, but for vestigial winged F_2's are presented in Tables VIII and IX.

The l_x' lines for the three total groups and the original vestigial parent stock are shown graphically in Fig. 3.

TABLE VIII

DEATH AND SURVIVORSHIP DISTRIBUTION FOR VESTIGIAL F_2 FLIES, DERIVED FROM *inter se* MATINGS OF F_1

Age in Days	P × P (5)				P ♂ × Z ♀ (3)	Z ♂ × P ♀ (3)	P × Z (3)		Z × Z (7)				All F_1 *Inter Se* Matings	
	Mating 73	Mating 75	Total		Mating 76	Mating 77	Total		Mating 72	Mating 74	Total		72–77	
	d_x'	d_x'	d_x'	l_x'	d_x'	d_x'	d_x'	l_x'	d_x'	d_x'	d_x'	l_x'	d_x'	l_x'
1– 2	1	3	4	1,000	1	1	2	1,000	5	2	7	1,000	13	1,000
3– 5	2	18	20	937	2	2	4	955	12	3	15	829	39	912
6– 8	—	3	3	619	—	1	1	864	1	—	1	463	5	649
9–11	—	8	8	571	1	3	4	841	1	2	3	439	15	615
12–14	1	2	3	444	—	2	2	750	—	2	2	366	7	514
15–17	1	5	6	397	—	4	4	705	—	2	2	317	12	466
18–20	—	1	1	317	—	8	8	614	—	—	—	268	9	385
21–23	—	10	10	302	2	5	7	432	—	1	1	268	18	324
24–26	—	5	5	127	2	3	5	273	—	2	2	244	12	203
27–29	—	1	1	48	2	3	5	159	—	3	3	195	9	122
30–32	—	—	—	32	—	1	1	45	—	3	3	122	4	61
33–35	1	—	1	32	—	1	1	23	—	—	—	49	2	34
36–38	—	—	—	16	—	—	—	0	—	—	—	49	—	20
39–41	1	—	1	16	—	—	—	—	—	—	—	49	1	20
42–44	—	—	—	0	—	—	—	—	—	—	—	49	—	14
45–47	—	—	—	—	—	—	—	—	—	2	2	49	2	14
48–50	—	—	—	—	—	—	—	—	—	—	—	0	—	0
Totals	7	56	63	—	10	34	44	—	19	22	41	—	148	—

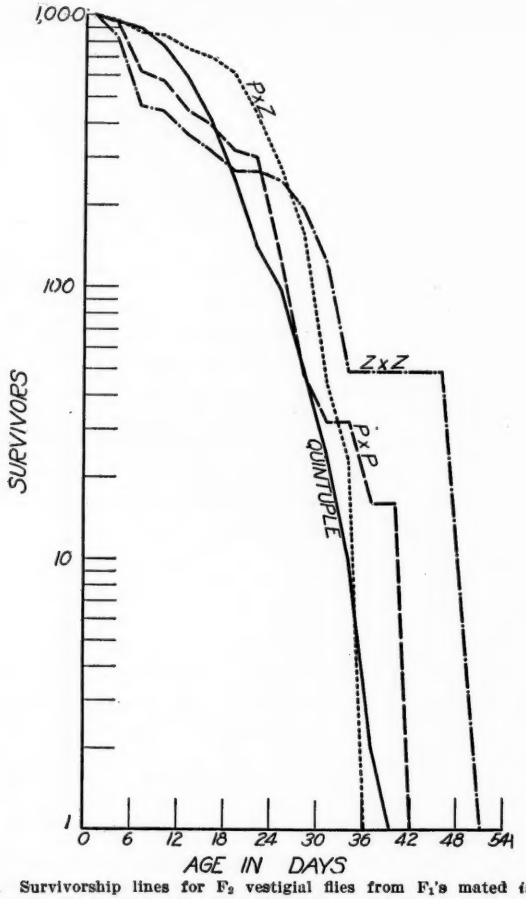


FIG. 3. Survivorship lines for F_2 vestigial flies from F_1's mated *inter se*. Dash line = P × P; dot line = P × Z; dash-dot line = Z × Z; solid line = original vestigial parent stock.

From these data we note:

1. Taking all vestigial F_2 flies from *inter se* matings together, the distribution of mortality agrees in an extraordinarily close manner with that of the original vestigial parent stock (*cf.* Tables III and IV). The mean duration of life of the original vestigial parent stock was $14.08 \pm .23$ days and that of the F_2 vestigials from *inter se* matings is $14.60 \pm .57$ days. The segrega-

tion in respect of mean longevity is plainly exact and precise. The variability, both absolute and relative, is probably significantly higher in the F_2 than in the P flies (vestigials), but the F_2 samples are not large and too much stress is not to be laid upon these differences.

TABLE IX

BIOMETRIC CONSTANTS FOR DURATION OF LIFE OF VESTIGIAL F_2 FLIES FROM *inter se* MATINGS OF F_1

Mating	Type	Mean Age at Death	Standard Deviation	Coefficient of Variation
P × P (Total)	(5)	13.10± .79 days	9.26± .54 days	70.70± 6.01
P ♂ × Z ♀ (76)...	(3)	17.45±2.18 days	10.23±1.54 days	58.64±11.49
Z ♂ × P ♀ (77)...	(3)	18.81± .89 days	7.67± .63 days	40.78± 3.85
P × Z (Total)	(3)	18.50± .85 days	8.34± .60 days	45.09± 3.85
Z × Z (Total)	(7)	13.15±1.31 days	12.46± .93 days	94.78±11.81
All *inter se* matings.	(5)+(3)+(7)	14.60± .57 days	10.31± .40 days	70.65± 3.91

2. The similar mating types (P × P and Z × Z) give identical results in mean and variability (having regard to the probable error involved) in respect of duration of life. This agrees with the previous findings for the case of wild type F_2 flies.

3. The *inter se* cross mating, P × Z, gives vestigial progeny flies having a significantly ***higher*** mean duration of life than either of the other two types (P × P, Z × Z). The differences with their probable errors are:

$$\text{For P} \times \text{P},\ 18.50 - 13.10 = 5.40 \pm 1.16 \text{ days}$$
$$\text{For Z} \times \text{Z},\ 18.50 - 13.15 = 5.35 \pm 1.56 \text{ days}$$

While these are not as large as the reverse differences found above in the case of the wild type F_2 flies, nevertheless they may be safely regarded, we think, as statistically significant.

The bearing of these differences between the several mating types upon the general problem of the inheritance of duration of life will be discussed further on.

The data regarding duration of life in the F_2 individuals produced by back crossing F_1 upon the parental types are given in Tables X and XI for wild type flies, and Tables XII and XIII for vestigial flies.

TABLE X

DEATH AND SURVIVORSHIP DISTRIBUTIONS FOR WILD TYPE F_2 FLIES, DERIVED FROM BACK CROSSES OF F_1 ON THE PARENTAL STOCKS

Age in Days	Z × Old Falmouth (8) (Reciprocally)				P × Old Falmouth (4) (Reciprocally)				All Back-crosses of F_1 on Wild Type		Z × Vestigial (2) (Reciprocally)				P × Vestigial (6) (Reciprocally)				All Back-crosses of F_1 on Vestigial	
	Mating 80	Mating 81	Total		Mating 84	Mating 85	Total		Matings 80+81+84 +85		Mating 78	Mating 79	Total		Mating 82	Mating 83	Total		Matings 78+79+82 +83	
	d_x'	d_x'	d_x'	l_x'	d_x'	d_x'	d_x'	l_x'	d_x'	l_x'	d_x'	d_x'	d_x'	l_x'	d_x'	d_x'	d_x'	l_x'	d_x'	l_x'
1– 5.....	6	7	13	1,000	—	2	2	1,000	15	1,000	—	3	3	1,000	—	—	—	1,000	3	1,000
6–11.....	5	28	33	959	1	25	26	995	59	978	—	2	2	966	5	3	8	1,000	10	986
12–17.....	2	—	2	855	4	5	9	923	11	891	5	3	8	943	2	8	10	938	18	940
18–23.....	34	21	55	849	13	11	24	899	79	875	3	3	6	852	13	7	20	860	26	857
24–29.....	16	24	40	675	51	26	77	833	117	760	10	3	13	784	18	6	24	705	37	737
30–35.....	35	19	54	549	23	13	36	622	90	588	15	2	17	636	17	18	35	519	52	567
36–41.....	7	13	20	379	20	15	35	523	55	456	16	4	20	443	3	6	9	248	29	327
42–47.....	10	12	22	315	16	28	44	427	66	375	7	2	9	216	4	4	8	178	17	194
48–53.....	15	13	28	246	11	18	29	307	57	279	4	1	5	114	3	—	3	116	8	115
54–59.....	3	28	31	158	16	53	69	227	100	195	3	1	4	57	7	1	8	93	12	78
60–65.....	9	9	18	60	7	4	11	38	29	48	1	—	1	11	2	1	3	31	4	23
66–71.....	—	1	1	3	1	2	3	8	4	6	—	—	—	0	1	—	1	8	1	5
72–77.....	—	—	—	0	—	—	—	0	—	0	—	—	—	—	—	—	—	0	—	0
Totals....	142	175	317	—	163	202	365	—	682	—	64	24	88	—	75	54	129	—	217	—

TABLE XI

BIOMETRIC CONSTANTS FOR DURATION OF LIFE OF WILD TYPE F_2 FLIES FROM BACK CROSSES

Matings	Type	Mean Age at Death	Standard Deviation	Coefficient of Variation
Wild ♂ × Z ♀ (80)	(8)	32.56± .83 days	14.67± .59 days	45.07±2.14
Z ♂ × wild ♀ (81)	(8)	33.91± .93 days	18.19± .66 days	53.64±2.43
Total Z × wild	(8)	33.30± .63 days	16.72± .45 days	50.20±1.65
Wild ♂ × P ♀ (84)	(4)	36.57± .68 days	12.85± .48 days	35.13±1.47
P ♂ × wild ♀ (85)	(4)	38.83± .82 days	17.31± .58 days	44.59±1.77
Total P × wild....	(4)	37.82± .55 days	15.52± .39 days	41.03±1.18
Total back cross on wild.....	(8)+(4)	35.72± .42 days	16.25± .30 days	45.48± .99
Vestigial ♂ × Z ♀ (78).....	(2)	35.63± .91 days	10.81± .64 days	30.34±1.97
Z ♂ × Vestigial ♀ (79).....	(2)	26.56±2.11 days	15.29±1.49 days	57.57±7.23
Total Z × Vestigial	(2)	33.15± .92 days	12.85± .65 days	38.75±2.25
Vestigial ♂ × P ♀ (82).....	(6)	32.52±1.09 days	14.05± .77 days	43.22±2.79
P ♂ × Vestigial ♀ (83).....	(6)	29.33±1.05 days	11.46± .74 days	39.05±2.90
Total P × Vestigial	(6)	31.19± .78 days	13.12± .55 days	42.08±2.06
Total back cross of vestigial.....	(2)+(6)	31.98± .60 days	13.05± .42 days	40.80±1.53

From Tables X–XIII we note the following points:

1. There is evident a general degradation of mean duration of life in back-cross flies, whether compared with original parents, F_1's or *inter se* F_2's. Thus we have the following system of differences:

Original wild parent — all wild type flies from back crosses of F_1 on wild = 44.26 — 35.72 = 8.54 ± .61

Original wild parent — all wild type flies from back crosses of F_1 on vestigial = 44.26 — 31.98 = 12.28 ± .74

Original vestigial parent — all vestigial flies from back crosses of F_1 on vestigial = 14.08 — 12.84 = 1.24 ± .36

There can be no doubt about a significant lowering of mean duration of life of these back-cross flies as compared with their original progenitors in the P generations. In the worst case (the last) the difference is 3.4 times its probable error.

In the case of F_1 flies it is idle to take the differences here because the F_1's are longer lived (as we have already seen) than the wild type original parent. Therefore the differences between F_1 and back crosses must of necessity be larger than those we have just examined.

TABLE XII

DEATH AND SURVIVORSHIP DISTRIBUTIONS FOR VESTIGIAL F_2 FLIES, DERIVED FROM BACK CROSSES OF F_1 ON QUINTUPLE STOCK

Age in Days	Z × Vestigial (2) (Reciprocally)				P × Vestigial (6) (Reciprocally)				All Back-crosses of F_1 on Vestigial		All F_1 ♂ × Vest. ♀		All Vestigial ♂ × F_1 ♀	
	Mating 78	Mating 79	Total		Mating 82	Mating 83	Total		Matings 78+79+82+83		Matings 79+83		Matings 78+82	
	d_x'	d_x'	d_x'	l_x'	d_x'	d_x'	d_x'	l_x'	d_x'	l_x'	d_x'	l_x'	d_x'	l_x'
1– 2	1	2	3	1,000	1	2	3	1,000	6	1,000	4	1,000	2	1,000
3– 5	6	12	18	974	5	14	19	980	37	977	26	968	11	986
6– 8	3	6	9	819	10	22	32	853	41	838	28	756	13	908
9–11	11	7	18	741	15	16	31	640	49	684	23	532	26	817
12–14	11	6	17	586	19	15	34	433	51	500	21	347	30	634
15–17	15	3	18	440	8	4	12	207	30	308	7	177	23	423
18–20	4	3	7	284	8	4	12	127	19	195	7	121	12	261
21–23	8	2	10	224	2	2	4	47	14	124	4	65	10	176
24–26	5	1	6	138	1	—	1	20	7	71	1	32	6	106
27–29	6	1	7	86	1	—	1	13	8	45	1	24	7	63
30–32	1	—	1	26	—	—	—	7	1	15	—	16	1	14
33–35	1	—	1	17	—	1	1	7	2	11	1	16	1	7
36–38	—	1	1	9	—	—	—	0	1	4	1	8	—	0
39–41	—	—	—	0	—	—	—	—	—	0	—	0	—	—
Totals	72	44	116	—	70	80	150	—	266	—	124	—	142	—

TABLE XIII

BIOMETRIC CONSTANTS FOR DURATION OF LIFE OF VESTIGIAL F_2 FLIES FROM BACK CROSSES

Mating	Type	Mean Age at Death	Standard Deviation	Coefficient of Variation
Vestigial ♂ × Z ♀ (78)	(2)	16.47±.59 days	7.41±.42 days	45.01±3.00
Z ♂ × Vestigial ♀ (79)	(2)	11.41±.78 days	7.64±.55 days	66.92±6.63
Total Z × Vestigial	(2)	14.55±.49 days	7.89±.35 days	54.22±3.03
Vestigial ♂ × P ♀ (82)	(6)	12.86±.42 days	5.20±.30 days	40.44±2.66
P ♂ × Vestigial ♀ (83)	(6)	10.33±.41 days	5.37±.29 days	52.06±3.45
Total P × Vestigial	(6)	11.51±.30 days	5.44±.21 days	47.30±2.22
Total back crosses on Vestigial	(2)+(6)	12.84±.28 days	6.79±.20 days	52.91±1.93
Total F_1 ♂ × Vestigial ♀	—	10.71±.38 days	6.29±.27 days	58.75±3.27
Total Vestigial ♂ × F_1 ♀	—	14.69±.38 days	6.67±.27 days	45.38±2.16

For the F_2's from *inter se* matings of F_1 we have the following:

F_2 (from P × P) wild type — wild type from back cross P × wild
$= 46.34 - 37.82 = 8.52 \pm .91$

F_2 (from Z × Z) wild type — wild type from back cross Z × wild
$= 46.01 - 33.30 = 12.71 \pm .96$

F_2 (from P × Z) wild type — wild type from all back crosses on wild
$= 37.66 - 35.72 = 1.94 \pm .77$

F_2 (from P × P) wild type — wild type from back cross P × vestigial
$= 46.34 - 31.19 = 15.15 \pm 1.07$

F_2 (from P × Z) wild type — wild type from all back crosses on vestigial
$= 46.01 - 33.15 = 12.86 \pm 1.17$

F_2 (from P × Z) wild type — wild type from all back crosses on vestigial
$= 37.66 - 31.98 = 5.68 \pm .88$

Thus it is clear that the wild type F_2 flies from back crosses of F_1 upon either original parent have a significantly lower mean duration of life than do the F_2 flies from *inter se* matings of F_1. The only exception to this rule is found in the case of the F_2 from the P × Z matings, when compared with all back crosses upon wild. This difference is less than three times its probable error.

Turning now to vestigials we have:

F_2 (from P × P) vestigial — vestigial from back cross P × vestigial
$= 13.10 - 11.51 = 1.59 \pm .54$
F_2 (from Z × Z) vestigial — vestigial from back cross Z × vestigial
$= 13.15 - 14.55 = -1.40 \pm 1.40$
F_2 (from P × Z) vestigial — vestigial from all back crosses on vestigial
$= 18.50 - 12.84 = 5.66 \pm .89$

Here the only difference which is significant is the last, which involves the P × Z F_1 flies. Everywhere this group gives an aberrant result.

2. There are certain definite and orderly differences in mean duration of life between the flies from the two moieties of otherwise identical reciprocal back crosses, and also between the flies coming from back crosses involving the two sorts of F_1's, namely P and Z. These differences are as follows:

WILD TYPE FLIES

(Wild ♂ × Z ♀) — (Wild ♂ × P ♀)	$= 32.56 - 36.57 = -4.01 \pm 1.07$
(Z ♂ × Wild ♀) — (P ♂ × Wild ♀)	$= 33.91 - 38.83 = -4.92 \pm 1.24$
(Vest. ♂ × Z ♀) — (Vest. ♂ × P ♀)	$= 35.63 - 32.52 = +3.11 \pm 1.42$
(Z ♂ × vest. ♀) — (P ♂ × vest. ♀)	$= 26.56 - 29.33 = -2.77 \pm 2.36$

VESTIGIAL FLIES

(Vest. ♂ × Z ♀) — (Vest. ♂ × P ♀)	$= 16.47 - 12.86 = +3.61 \pm .72$
(Z ♂ × vest. ♀) — (P ♂ × vest. ♀)	$= 11.41 - 10.33 = +1.08 \pm .88$

From these differences it appears that when the back-cross mating is such as to produce only wild type flies the offspring are significantly longer lived when the F_1 parent is of P origin than when it is of Z origin. The reverse *appears* to be true when the mating is of the sort to produce both wild and vestigial types in the offspring, though most of the series here are unfortunately too short to give statistically significant differences.

The differences between reciprocal matings are as follows:

WILD TYPE FLIES

(Wild ♂ × Z ♀) — (Z ♂ × wild ♀)	$= 32.56 - 33.91 = -1.35 \pm 1.25$
(Wild ♂ × P ♀) — (P ♂ × wild ♀)	$= 36.57 - 38.83 = -2.26 \pm 1.07$
(Vest. ♂ × Z ♀) — (Z ♂ × vest. ♀)	$= 35.63 - 26.56 = +9.07 \pm 2.30$
(Vest. ♂ × P ♀) — (P ♂ × vest. ♀)	$= 32.52 - 29.33 = +3.19 \pm 1.51$

VESTIGIAL FLIES

(Vest. ♂ × Z ♀) — (Z ♂ × vest. ♀)	$= 16.47 - 11.41 = +5.06 \pm .98$
(Vest. ♂ × P ♀) — (P ♂ × vest. ♀)	$= 12.86 - 10.33 = +2.53 \pm .49$

From these data it appears that in back crosses of F_1 on wild the offspring tend to be *longer* lived (though because of the shortness of the series neither difference is significant) when the *mother* is pure wild: in back crosses of F_1 on vestigial, the offspring, whether wild or vestigial, are *shorter* lived when the *mother* is pure *vestigial.* All the differences but one are clearly significant, and that one is probably so. There thus appears here a definite matroclinal tendency relative to the inheritance of duration of life.

F_3 Generation

The matings made to produce F_3 flies were few in number, as is shown in Table II, and covered only a small fraction of the possibilities. In Table XIV are given the Mendelian results, relative to the segregation of normal and vestigial wing, for all the matings it was possible to use. The other matings indicated in Table II could not be used in the analysis, because they were mass matings in which a fly might be either heterozygous or pure dominant, and as a matter of fact some were heterozygous, as indicated by the results, in the case of the three matings not included in Table XIV.

Because of interest in their apparently aberrant behavior, already brought out, attention was confined in making up the matings for F_3 to the F_2 produce of $P \times Z$ matings.

It will be seen from Table XIV that in every case of matings involving vestigial F_2 females (which includes all matings in the table except the last) there is an *excess* of *vestigial flies* in the offspring, over what would be expected on Mendelian theory. The discrepancies are certainly significant in the totals, and also for two out of the four separate matings. It will be recalled that Table V shows an excess of vestigials from the back crosses of F_1 on the parent stocks.

Tables XV–XVIII inclusive give the F_3 results as to duration of life.

TABLE XIV

MENDELIAN SEGREGATION IN F_2 OF NORMAL AND VESTIGIAL WINGS, TABULATED BY SEPARATE MATINGS

Mating Type	Number of F_2 Flies with Wings			Probable Error	Deviation / P.E. Dev.	Probable Times of Occurrence of Such a Deviation in 100 Trials	Mating No.
	Normal	Vestigial	Total				
Vestigial ♀ ♀							
(54) Z ♂ × D (76) ♀ .	76	121	197				86
Expected.....	*98.5*	*98.5*	*197*	±4.73	4.8	.12	
(54) Z ♂ × D (77) ♀ .	67	76	143				90
Expected.....	*71.5*	*71.5*	*143*	±4.03	1.1	45.81	
(54) Total.....	143	197	340				86+90
Expected.....	*170*	*170*	*340*	±6.22	4.3	.37	
(52) P ♂ × D (76) ♀ .	95	107	202				88
Expected.....	*101*	*101*	*202*	±4.79	1.3	38.06	
(52) P ♂ × D (77) ♀ .	63	119	182				92
Expected.....	*91*	*91*	*182*	±4.55	6.2	.005	
(52) Total.....	158	226	384				88+92
Expected.....	*192*	*192*	*384*	±6.61	5.1	.07	
Wild type ♀ ♀ ...							
(52) P ♂ × D (76) ♀ .	175	0	175				89
Expected.....	*175*	*0*	*175*	—	—	—	—

TABLE XV

DEATH AND SURVIVORSHIP DISTRIBUTIONS FOR WILD TYPE F_2 FLIES

Age in Days	Z F_1 ♂ × Vestigial D F_2 ♀				P F_1 ♂ × Vestigial D F_2 ♀				P F_1 ♂ × Wild Type D F_2 ♀	
	Mating 86	Mating 90	Total		Mating 88	Mating 92	Total		Mating 89	
	d_x'	d_x'	d_x'	l_x'	d_x'	d_x'	d_x'	l_x'	d_x'	l_x'
1– 5..	1	1	2	1,000	11	3	14	1,000	2	1,000
6–11..	5	2	7	986	6	8	14	911	6	989
12–17..	9	13	22	937	10	6	16	823	26	954
18–23..	18	24	42	783	21	9	30	722	35	806
24–29..	5	11	16	490	13	4	17	532	12	606
30–35..	5	9	14	378	5	6	11	424	23	537
36–41..	6	2	8	280	6	6	12	354	14	406
42–47..	6	1	7	224	6	4	10	278	29	326
48–53..	15	2	17	175	14	12	26	215	18	160
54–59..	6	2	8	56	3	5	8	51	10	57
60–65..	—	—	—	0	—	—	—	0	—	0
66–71..	—	—	—	—	—	—	—	—	—	—
Totals .	76	67	143	—	95	63	158	—	175	—

TABLE XVI

BIOMETRIC CONSTANTS FOR DURATION OF LIFE OF WILD TYPE F_3 FLIES

Mating	Type	Mean Age at Death	Standard Deviation	Coefficient of Variation
Z F_1 ♂ × Vest. D_{76} F_2 ♀ (86).	(54)	32.53±1.22	15.74± .86	48.37±3.21
Z F_1 ♂ × Vest. D_{77} F_2 ♀ (90).	(54)	24.68± .87	10.55± .61	42.80±2.92
Total Z F_1 ♂ × Vest. D ♀ ...	(54)	28.85± .80	14.11± .56	48.91±2.37
P F_1 ♂ × Vest. D_{76} F_2 ♀ (88).	(52)	27.25±1.10	15.88± .78	58.29±3.70
P F_1 ♂ × Vest. D_{77} F_2 ♀ (92).	(52)	31.40±1.44	16.90±1.02	53.83±4.07
Total P F_1 ♂ × Vest. D ♀ ...	(52)	28.90± .88	16.42± .62	56.82±2.77
P F_1 ♂ × Wild type D_{76} F_2 ♀ (89)	(52)	32.05± .72	14.18± .51	44.26±1.88

TABLE XVII

DEATH AND SURVIVORSHIP DISTRIBUTIONS FOR VESTIGIAL F_3 FLIES

Age in Days	Z F_1 ♂ × Vestigial D F_2 ♀				P F_1 ♂ × Vestigial D F_2 ♀			
	Mating 86	Mating 90	Total		Mating 88	Mating 92	Total	
	d_x'	d_x'	d_x'	l_x'	d_x'	d_x'	d_x'	l_x'
1– 2.....	45	12	57	1,000	22	21	43	1,000
3– 5.....	50	25	75	711	16	27	43	810
6– 8.....	7	21	28	330	12	19	31	619
9–11.....	9	7	16	188	14	15	29	482
12–14.....	5	4	9	107	22	34	56	354
15–17.....	1	7	8	61	16	3	19	106
18–20.....	2	—	2	20	2	—	2	22
21–23.....	—	—	—	10	—	—	—	13
24–26.....	1	—	1	10	—	—	—	13
27–29.....	1	—	1	5	—	—	—	13
30–32.....	—	—	—	0	—	—	—	13
33–35.....	—	—	—	—	1	—	1	13
36–38.....	—	—	—	—	2	—	2	9
Totals.....	121	76	197	—	107	119	226	—

TABLE XVIII

BIOMETRIC CONSTANTS FOR DURATION OF LIFE OF VESTIGIAL F_3 FLIES

Mating	Type	Mean Age at Death	Standard Deviation	Coefficient of Variation
Z F_1 ♂ × Vest. D_{76} F_2 ♀ (86).	(54)	5.28±.28	4.64±.20	87.95±6.09
Z F_1 ♂ × Vest. D_{77} F_2 ♀ (90).	(54)	7.07±.33	4.21±.23	59.60±4.26
Total Z F_1 × Vest. D ♀	(54)	5.97±.22	4.57±.16	76.49±3.83
P F_1 ♂ × Vest. D_{76} F_2 ♀ (88).	(52)	9.93±.45	6.98±.32	70.26±4.57
P F_1 ♂ × Vest. D_{77} F_2 ♀ (92).	(52)	8.17±.28	4.52±.20	55.29±3.07
Total P F_1 ♂ × Vest. D ♀ ...	(52)	9.00±.26	5.88±.19	65.30±2.82

The first point which will be noted from these Tables XV–XVIII is the still further marked degradation in duration of life of F_3 flies, as compared with those of earlier generations. None of the means approach in value the original parental stocks, and are even well below, taken as a whole, the F_2 flies from back crosses.

Another result is the system of differences, in the main significant, in duration of life according to whether the F_2 vestigial females used were from mating 76 or mating 77. D_{76} females came from $Z\,♂ \times P\,♀$, and D_{77} females came from $P\,♂ \times Z\,♀$. Now, when a $D_{76}\,♀$ was mated back to $Z\,♂$, the resulting wild type flies were longer lived and the vestigials were shorter lived than when a D_{77} female was mated to a $Z\,♂$. When these same two sorts of females were mated to a $P\,♂$ the offspring of the D_{77} females were longer lived if normal winged and shorter lived if vestigial winged than the offspring of the D_{76} females.

In the one mating (89) which enables a comparison of D_{76} wild type and a D_{76} vestigial each mated to the same type of male (P), the resulting wild type progeny are longer lived from the wild type mother. The difference 4.80 ± 1.31 days is almost certainly significant.

THE EFFECT OF ABSENCE OF WINGS ON DURATION OF LIFE

It can not fail to occur to one that perhaps the reason why vestigial winged flies are invariably short lived is merely and directly physiological, arising because such a fly has no *functional* wings and therefore can not fly, but has its activity confined to walking and jumping. Stated in extreme forms, the idea would be that so far as inherent constitutional factors influencing duration of life are concerned Quintuple and wild stocks are on the same footing, but because Quintuple has no functional wings it is physiologically unable so to conduct its life as to realize its constitutional potentialities in respect of longevity.

It is possible experimentally to test this idea, in part

at least. Suppose in a large number of wild type flies immediately after emergence the wings are cut off close to the body. Since they do not regenerate these flies must then go through life wingless. If then a duration of life experiment is carried through with them, and a life curve constructed, will this curve be like that for Quintuple flies, or will it be like that for normal wild flies? Or, put in another way, what difference in the distribution of mortality of *Drosophila* does the presence or absence of wings make in a purely physiological, somatic sense?

This experiment we have carried out on a large scale twice. Unfortunately we can give here the result only of the second of these investigations, because in the case of the first series all the surviving flies were destroyed when rather more than half way through the life curve, owing to the accidental misbehavior of the regulating apparatus of the incubator in which they were. The results, however, so far as they went were in entire agreement with those here presented.

The flies in this experiment emerged April 16–19, 1922, from 25 mass matings (2 pairs each) Old Falmouth stock, line 107, generation 26. Progeny were taken from the mating bottles at 24-hour intervals and etherized. Only the flies whose wings were fully expanded and dried were used, in either experimental or control group. With fine scissors both wings were clipped off as close to the thorax as possible, care being taken to avoid injury to the halteres. The experimental and control bottles—with 30 flies in each bottle—were made up alternately to distribute the flies at random. Both sets were then put through a standard duration of life test at 25° C. in the usual way in which all our work is done, with the results shown in Tables XIX and XX and Fig. 4.

From the results it is evident that surgical removal of the normal wings of wild type flies at the time of emergence somewhat shortens duration of life, but to no such

TABLE XIX

DEATH AND SURVIVORSHIP DISTRIBUTIONS FOR WILD TYPE FLIES (*a*) WITH WINGS SURGICALLY REMOVED, AND (*b*) WITH NORMAL WINGS

Age in Days	Normal Wings		Wings Removed	
	d_x'	l_x'	d_x'	l_x'
1– 3	5	1,000	4	1,000
4– 6	2	990	10	992
7– 9	4	986	20	973
10–12	4	979	9	934
13–15	9	971	34	917
16–18	12	953	30	852
19–21	22	930	45	794
22–24	22	887	38	707
25–27	17	844	26	634
28–30	33	811	37	584
31–33	21	747	21	513
34–36	20	706	22	472
37–39	26	667	19	430
40–42	33	618	21	393
43–45	34	553	26	353
46–48	34	486	24	303
49–51	33	420	20	256
52–54	42	356	32	218
55–57	64	274	28	156
58–60	25	150	27	102
61–63	20	101	11	50
64–66	12	62	9	29
67–69	5	39	1	12
70–72	8	29	3	10
73–75	2	14	1	4
76–78	4	10	1	2
79–81	—	2	—	0
82–84	1	2	—	0
85–87	—	0	—	0
Totals	514	—	519	—

TABLE XX

BIOMETRIC CONSTANTS FOR DURATION OF LIFE IN WILD TYPE FLIES (*a*) WITH WINGS SURGICALLY REMOVED, AND (*b*) WITH NORMAL WINGS

Group	Mean Duration of Life	Standard Deviation	Coefficient of Variation
Wings removed	34.56±.50 days	17.01±.36 days	49.23±1.26
Normal wings	43.26±.47 days	15.69±.33 days	36.27± .86

extent as would be required to account for the normal difference between wild and Quintuple stocks in this respect. The differences between clipped and unclipped groups are significant in comparison with their prob-

able errors, but the difference between the means is only about one fourth of the difference between wild and Quintuple means.

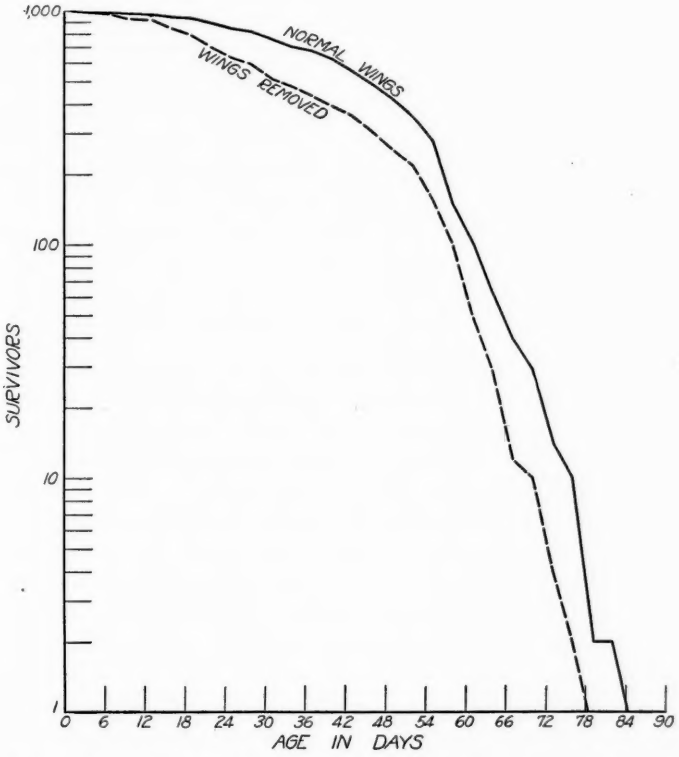


FIG. 4. Survivorship lines for normal wild type flies (solid lines) and flies of same stock with wings removed at emergence (broken lines).

It may be safely concluded that the difference between wild and Quintuple stocks in respect of duration of life is not solely due to the fact that the Quintuple have no functional wings while the wild do. One perhaps could reasonably have concluded this on general grounds, but it seemed well to have an experimental proof. Certainly a considerable part of the difference between

clipped and unclipped shown in the data, and perhaps nearly all of it, is due to the unavoidable and unperceived gross injury to the fly at the time of the operation. Three times as many clipped as unclipped died during the first 10 days of life. No effort was made at the operation to do anything to the wing stumps to prevent loss of body fluids. We have in the results the maximum effect of *both* absence of wings throughout life, and a rather rough major surgical operation at the start of life. If the second of these two factors could be eliminated and leave the first by itself alone, it is probable that the two curves of Fig. 4 would be insignificantly different from each other.

Discussion of Results

So far we have studiously avoided any discussion of the meaning of the results, desiring to present the objective facts separated clearly from any interpretation of them. We wish now to enter upon a brief discussion of the meaning of what we have found, prefacing our remarks in this direction by the statement that we regard this investigation as in no way final, but rather as preliminary to a series (probably long) of experimental studies which must be made before anything like a complete understanding of the mechanism of inheritance of duration of life in *Drosophila* will be possible.

For convenience in discussion we have summarized all our experiments in the form of pedigree diagrams in Figs. 5–17, entering beside each designation of the type of fly the mean duration of life of that group to the nearest whole number of days.

With the data before us we may point cut the broad results of the investigation. These seem to us to be:

1. Duration of life behaves in the F_1, F_2 and a part of the possible F_3 offspring from reciprocal crosses of short-lived and long-lived strains of *Drosophila* as any character of the organism would be expected to behave if it were inherited in a Mendelian manner. There is a

somewhat higher duration of life in F_1 than in either of the parent stocks (effect of heterosis). There is a clear-cut segregation of long-lived and short-lived groups in subsequent generations.

2. In its genetic behavior duration of life is completely and invariably associated with certain morphological characteristics of the flies, in the sense that no vestigial-winged fly has ever been found to be long-lived, and no group of normal-winged flies have ever

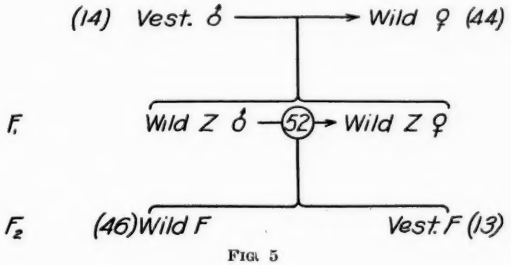


FIG. 5

been found to have a life curve even approaching in form that which is characteristic of vestigial-winged flies.

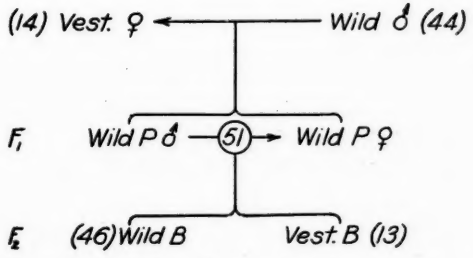


FIG. 6

There are three possible interpretations of these results which suggest themselves in the light of our present knowledge of, and viewpoint about, genetic phenomena in general. These are:

1. It may be assumed that duration of life is deter-

mined by a single Mendelian gene, completely or perfectly linked to the gene for vestigial, so that crossing over never occurs between the former and the latter.

2. It may be assumed that duration of life is a character, like body size, controlled by n factors, each of which Mendelizes. This postulates what amounts to a whole flock of genes for viability in a graded series, such that the effect of each translates itself into actuality at varying points in the entire span of imaginal life.[2]

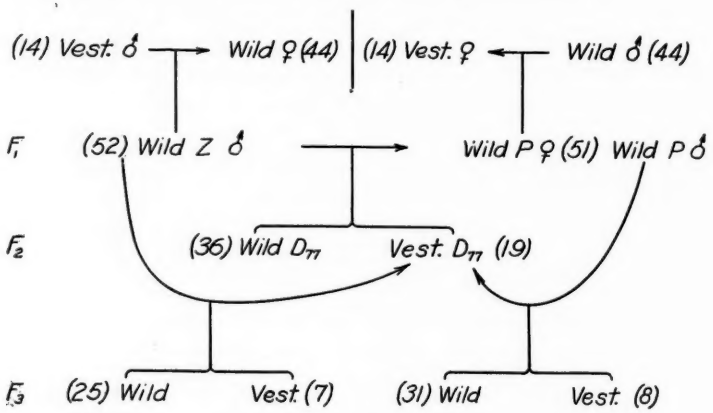


FIG. 7

3. *It may be assumed that duration of life is not in and of itself a separate and different character of the organism, but instead is simply the expression in time of the organization of the body,* which organization may be regarded as physico-chemical, structural, physiological or functional, depending upon which of the aspects of organization we may at the time be emphasizing.

[2] Obviously if we are to have viability or lethal genes at all there is no reason why we should suppose them confined to embryonic, or larval, or pupal stages of the life history. A gene that kills at age 50 days is just as easily conceived, and for all we know just as probable *a priori*, as one that kills 2-day-old larvæ. Presumably what a lethal gene means biologically is merely that it determines an organization of the body such that viability ceases (or put the other way about, that the individual cannot go on living) after that organization (structural or functional) has attained its full somatic development.

Of these alternative hypotheses the first may be dismissed at once for two reasons, first because it is inherently improbable biologically, and second because, as will be demonstrated in the next following paper in this series, the same kind of evidence as that adduced in this paper can be brought forward to indicate a separate gene for duration of life completely linked to the genes for each one of a whole series of morphological characters, such as eye color and the like.

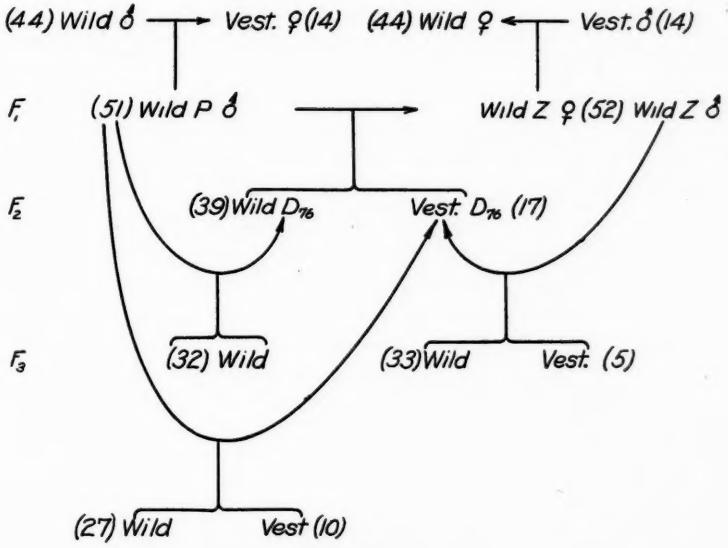


FIG. 8

Regarding the second hypothesis it may be said to violate the logical principle *Entia non sunt multiplicanda præter necessitatem.* For why should we postulate a series of *special* genes for duration of life, each necessarily (because of the observed facts) completely associated or linked with genes for morphological characters. To do so seems to us to serve no useful purpose.

With the third hypothesis, which has been discussed by one of us elsewhere (52), the existing knowledge

seems to be in general in entire accord. It means that in a strict sense we can not speak of the inheritance of duration of life any more properly than we can speak of the inheritance of tuberculosis.[3]

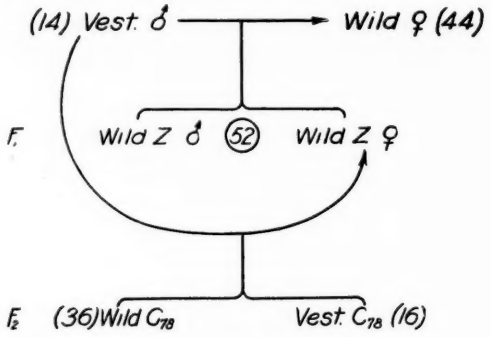


FIG. 9

What is inherited in both cases is not the thing itself, but the bodily organization, of which duration of life, on the one hand, and the disease tuberculosis, on the other hand, are in part the manifestations. In short what is

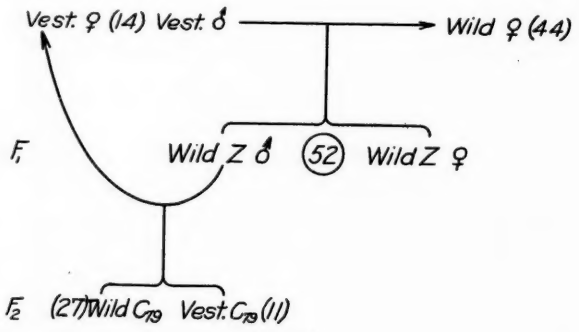


FIG. 10

[3] Actually it is convenient to speak of the inheritance of duration of life, just as it is to say that tuberculosis is in some degree inherited. And no harm can be done by such usage of words, provided one understands that it is merely a verbal economy, to save the use of a longer and more awkward phrase.

inherited is the *diathesis* for longevity, not longevity itself. Put in another way, what this view of the matter says is that if the duration of an individual's life is an implicit function of the individual's organization or constitution (a purely physical thing fundamentally) which

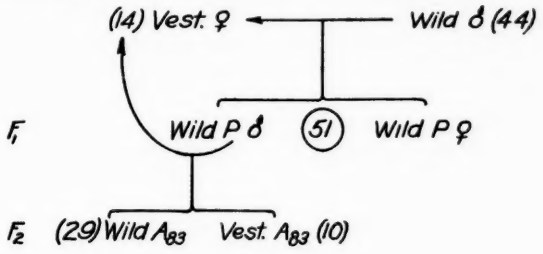


FIG. 11

is inherited, it follows that duration of life will behave exactly as though it were itself inherited. It then directly follows that, from the standpoint of methodology, we may by a genetic study of duration of life get valuable knowledge as to the mode or form of the functional

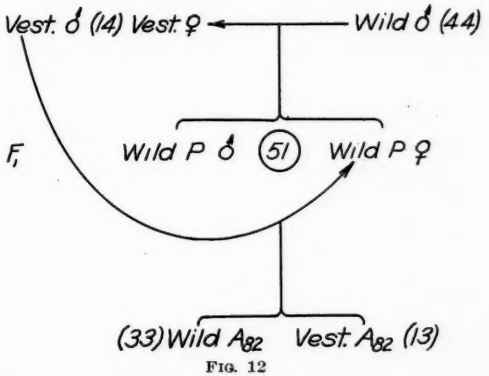


FIG. 12

relationship between physical organization and duration of life, which in fact is thus perceived from a new angle to be the fundamental problem involving duration of life.

This means that in the present series of experiments we have demonstrated that the gene for vestigial, besides affecting the form, size and general functional organization of the wings of *Drosophila, also* influences,

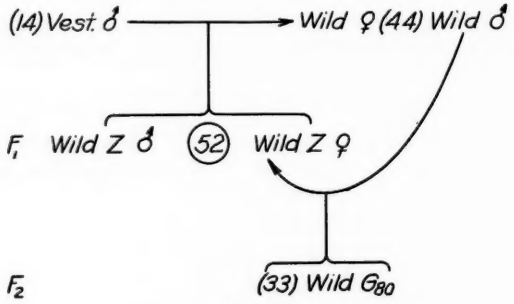


FIG. 13

in and through its effects on the whole organization of every fly in which it is present, the duration of life of that fly. We have measured with considerable exactness and manifoldness what the quantitative effect of

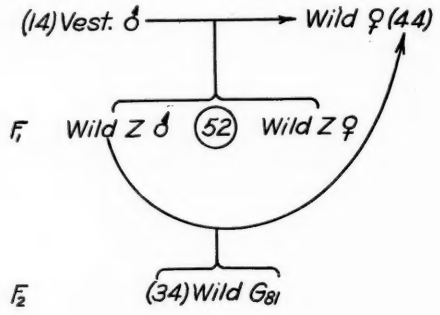


FIG. 14

this gene is upon duration of life (and, of course, at the same time the effect of its allelomorph the gene for normal wing).

This view of the case seems to us to be in accord with the best current opinion as to the biological meaning

of mutant genes generally. Thus Morgan (9, pp. 238–239) says:

> If we examine almost any mutant race, such as the race of white-eyed *Drosophila,* we find that the white eye is only one of the characteristics that such a mutant race shows. The productivity of the individual is also much affected, and the viability is lower than in the wild fly. All of these peculiarities are found whenever the white eye emerges from a cross and are not separable from the white-eyed condition. It follows that whatever it is in the germ-plasm that produces white eyes also produces other modifications as well, and modifies not only such "superficial" things as color, but also such "fundamental" things as productivity and viability. Many examples of this manifold effect are known to students of heredity.
>
> It is perhaps not going too far to say that any change in the germ-plasm may produce many kinds of effects on the body. Clearly then the character that we choose to follow in any case is only the most conspicuous or (for purposes of identification) the most striking or convenient modification that is produced. Since, however, these effects always go together, and can be explained by the assumption of a single unit difference in the germ-plasm, the particular difference in the germ-plasm is more significant than the character chosen as its index.

The general view as to the mechanism through which duration of life behaves as an inherited character which is here tentatively adopted has been discussed in more

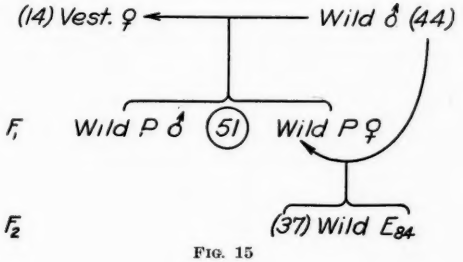


FIG. 15

detail by Pearl at various points in "The Biology of Death" (52). Thus it is there suggested (p. 212) that "what heredity does in relation to duration of life is chiefly to determine, within fairly narrow limits, the total

energy output which the individual can exhibit in its life time. This limitation is directly brought about presumably through two general factors: viz., (*a*) the kind or quality of material of which this particular vital machine is built, and (*b*) the manner in which the parts are put together or assembled."

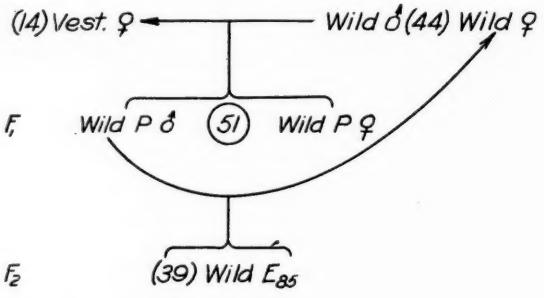


FIG. 16

In this statement (*a*) and (*b*) are equivalent to what is here, in more general terms, called "organization."

To come now to details of the present investigation there are a number of points for which we have no present explanation to offer. The chief of these are:

1. The significantly aberrant Mendelian ratios of vestigial.

2. The peculiar differences in duration of life, apparently associated with these departures from Mendelian expectation of vestigial. We refer to such matters as the divergent results of $Z \times P$ as compared with other *inter se* matings of F_1 to produce F_2; the peculiar behavior of duration of life in back crosses: the failure of reciprocal matings to give identical results, though all morphological mutants dealt with have their location in the second chromosome.

3. The steady degradation in mean duration of life after F_1.

The present material is inadequate to the solution of these difficulties. It has certain defects which contribute

heavily to this inadequacy. In the first place Quintuple carries 5 different mutations each one of which has *some* influence on duration of life, as will be demonstrated in the next following paper in this series. We took account of but one of these morphological characters (namely vestigial) in this study. In the second place the material is not large enough in mass to deal adequately with the kind of deviations from expectation that appeared. In subsequent investigations we hope to remedy these defects. In the meantime the present study has fulfilled, we believe, the highest pragmatic test of any genetic inquiry. Namely, we are now in a position to predict what the duration of life of a progeny group of *Drosophila* will be, from a knowledge of the duration of life of the parents.

Summary

In this study, involving the determination of the duration of life of 5,415 individual flies, a cross was made between a long-lived stock of *Drosophila* (Old Falmouth, wild type) and a short-lived stock (Quintuple). In the F_1 generations the progeny were somewhat longer lived than either parent stock. In F_2 there was a definite and clear-cut segregation in respect of duration of life, long-lived and short-lived groups reappearing, with virtually identical mean duration of life to those of the original parent stocks. In its genetic behavior duration of life was found to be completely and invariably associated with certain morphological characteristics of the organism, in the sense that no vestigial-winged fly has ever been found, in the entire experience of the laboratory, to be long-lived, and no group of normal-winged flies has ever been found to have a life curve even approaching in form that which is characteristic of vestigial-winged flies. The probable meaning of these results, in relation to genetic phenomena in general, is discussed.

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